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Intraspecific and Interspecific Variation in the  
*Cryptotis agrensis* Species Complex of  
Small-Eared Shrews (Insectivora: Soricidae), with the  
Description of a New Species from Colombia

Regal Ochoa  
Ruth L. M. Johnson

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## Zoology

NEW SERIES, NO. 74

### Intraspecific and Interspecific Variation in the *Cryptotis nigrescens* Species Complex of Small-Eared Shrews (Insectivora: Soricidae), with the Description of a New Species from Colombia

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*Back cover: Cryptotis colombiana*

# Intraspecific and Interspecific Variation in the *Cryptotis nigrescens* Species Complex of Small-Eared Shrews (Insectivora: Soricidae), with the Description of a New Species from Colombia

Neal Woodman and Robert M. Timm

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## Abstract

The *Cryptotis nigrescens* species complex of small-eared shrews previously was considered to consist of a single, wide-ranging species with three subspecies distributed from southern Mexico to Panama. Our study of the patterns of morphological variation within this complex indicates that it is much more diverse and speciose than earlier believed. The group includes populations that occur only at high elevations (> 500 m) as well as the only taxon in the genus restricted to elevations below 100 m. Based on our investigations, we recognize five species: *C. mayensis* occurs on the Yucatan Peninsula and is known from an isolated locality in Guerrero; *C. merriami* has a patchy distribution from Chiapas, Mexico, to northern Costa Rica; *C. nigrescens* inhabits conterminous highlands in Costa Rica and Panama; *C. mera* is known from two isolated mountaintops along the Panama/Colombia border; and we describe a new species from the Central Cordillera of Colombia, which extends the known distribution of the complex to the southeast. In addition, recent studies indicate that *C. hondurensis* and *C. magna* may be imbedded phylogenetically within the *C. nigrescens* complex.

## Resumen

*Cryptotis nigrescens* es un complejo de especies que solía considerarse como una sola especie con tres subespecies distribuidas a lo largo de América Latina desde el sur de México hasta Panamá. Nuestro estudio de patrones de variación morfológica en este complejo indica que es diverso y con más especies de las que se había pensado antes. El grupo incluye poblaciones que habitan solamente en elevaciones por encima de los 500 m, y también el único taxón en el género que está restringido a elevaciones bajo 100 m. Basados en nuestras investigaciones, reconocemos cinco especies. La primera, *C. mayensis*, se encuentra en la Península de Yucatán y en una localidad aislada en Guerrero, México. La segunda, *C. merriami*, tiene una distribución discontinua desde Chiapas en México hasta el norte de Costa Rica. La especie *C. nigrescens* habita en las cordilleras de Costa Rica y Panamá. Se sabe que *C. mera* vive en las cimas de dos montañas aisladas en la frontera entre Panamá y Colombia. La última es una especie nueva que describimos en esta publicación y que mora en la Cordillera Central de Colombia y que extiende la distribución del complejo hacia el sureste. Además, estudios recientes indican que las especies *C. hondurensis* y *C. magna* pueden estar relacionadas filogenéticamente con el complejo *C. nigrescens*.

## Introduction

Small-eared shrews of the genus *Cryptotis* have a wide distribution, occurring in parts of North America, Central America, and northwestern South

America. The genus reaches its greatest diversity in Mexico and Central America. Hall and Kelson (1959) recorded 25 species of *Cryptotis* in this region. In his revision of the Middle American *Cryptotis*, Choate (1970) recognized eight species of

small-eared shrews in Mexico and Central America, and his taxonomy has been followed by most subsequent authors, including Hall (1981), Honacki et al. (1982), Corbet and Hill (1991), and Wilson and Reeder (1993). We (Woodman & Timm, 1992, submitted) recognized four additional species from Guatemala, Honduras, and Mexico, bringing the total to 12 species.

One poorly understood Central American group of *Cryptotis* is the *C. nigrescens* complex, which was known to occur from Guerrero, Mexico, through Central America to the Panama/Colombia border. Most species of small-eared shrews that occur from central Mexico through northern South America are high-elevation forms, inhabiting regions over 500 m. The *C. nigrescens* complex, which includes both high-elevation and low-elevation taxa, is an exception. Choate (1970) provided the only recent comprehensive treatment of the taxonomy and distribution of *C. nigrescens*. He recognized one widely distributed species, *C. nigrescens*, which included three subspecies: *C. n. mayensis*, occurring on the Yucatan Peninsula and known from one locality in Guerrero, Mexico; *C. n. merriami*, which Choate described and is distributed from Chiapas, Mexico, to Honduras and El Salvador; and *C. n. nigrescens*, inhabiting Costa Rica and Panama to the Panama/Colombia border. Of the previously recognized species, Choate (1970) synonymized *C. mera*, *C. micrura*, *C. tersus*, and *C. zeteki* with *C. n. nigrescens*. *Cryptotis mayensis* was reduced to a subspecies of *C. nigrescens*.

In his review of the *Cryptotis* of Middle America, Choate (1970) had few complete specimens of *C. nigrescens*. Of the 237 *C. n. mayensis* available at that time, all but 10 were mandibles and partial crania from owl pellets, cave deposits, or Mayan ruins. Similarly, 15 of the 25 specimens available for *C. n. merriami* were from owl pellets, and only 24 skins with accompanying skulls of *C. n. nigrescens* were available for study. Recent collecting in Mexico has added important new specimens of *C. n. mayensis* and *C. n. merriami*, and work in Panama and Costa Rica has tremendously increased the number of *C. n. nigrescens* in museum collections. This wealth of new material led us to review this complex more thoroughly than was possible previously.

*Cryptotis nigrescens* was considered to be distinguished by its short rostrum; bulbous dentition; equal development of anterior and posterior portions of M1; unrecessed posterior margins of P4, M1, and M2; simple M3; and lack of an entoconid

in m3 (Choate, 1970). However, there is much variation in these characters both within this taxon and within the genus, and their polarizations are difficult to define.

Systematic relationships within the genus *Cryptotis* remain mostly unresolved. Woodman (1992) showed that the *C. nigrescens* group may be paraphyletic with respect to *C. hondurensis* and *C. magna*. *Cryptotis hondurensis* recently was described from montane pine forests in Honduras (Woodman & Timm, 1992). *Cryptotis magna* was described by Merriam (1895) from mountains of southern Oaxaca, Mexico. A more comprehensive redescription of this species was provided by Choate (1970), and it was illustrated by Robertson and Rickart (1975), who summarized its biology. In this paper, we use the “*C. nigrescens* group” to refer informally to only those shrews previously called *C. nigrescens*.

The purposes of this paper are to (1) revise the taxonomy and delineate the distributions of taxa previously included in *C. nigrescens*; (2) describe and illustrate a species new to science; and (3) review the available information on reproduction, elevational distribution, and habitat for the members of this complex.

## Methods

Cranial and mandibular measurements were recorded to the nearest 0.1 mm using either an ocular micrometer in a binocular microscope or a handheld dial caliper. Skin measurements are those recorded by the collector, except for head and body length (HB), which we calculated by subtracting the recorded tail length (TL) from the total length. All measurements are in millimeters. Dental terminology follows Choate (1970). The following craniomandibular measurements (fig. 1) were used in our analyses: condylobasal length, not including the upper incisors (CBL); cranial breadth (CB); breadth of zygomatic plate (ZP); interorbital breadth (IO); breadth of palate across first unicuspids (U1B); breadth of palate across third unicuspids (U3B); breadth of palate across second molars (M2B); palatal length (PL); upper tooth row length, U1 to M3, parallel to the long axis of the skull (TR); unicuspis tooth row length, parallel to the unicuspis tooth row (UTR); molariform tooth row length, P4 to M3, parallel to the long axis of the skull (MTR); posterior width of M1, across hypocone and metastyle (WM1); mandibular

length, from inferior sigmoid notch to posterior edge of mental foramen (ML); height of coronoid process (HCP); height of coronoid valley (HCV); height of articular condyle (HAC); breadth of articular condyle (BAC); articular condyle to posterior edge of m<sub>3</sub> (AC3); lower tooth row length, p<sub>3</sub> to m<sub>3</sub> (TRD); and length of lower first molar (m<sub>1L</sub>). Unless otherwise stated, univariate statistics are mean  $\pm$  standard deviation. All capitalized color names follow Ridgway (1912). Localities and elevations were taken directly from specimen tags and represent the descriptions of the original collectors. Corrections and additions are provided in brackets. We did not convert distances measured in miles or elevations measured in feet to the metric system to avoid inferring a level of accuracy greater than that originally recorded by the collector. Specimens from archeological or paleontological contexts were not used in statistical analyses or plotted on maps because of the possibility of temporal variation in size, shape, or geographic distribution. Number of specimens from archeological or paleontological sites is calculated as the minimum number of individuals.

Multivariate analyses were used to look at patterns of variation in overall similarity among specific members of the *C. nigrescens* complex. Although these analyses often are useful for distinguishing among known groups, and occasionally point out variables useful for distinguishing taxa, they were not relied upon to determine species or provide taxonomic diagnoses. In general, members of the *C. nigrescens* complex were found to be very conservative in overall form, particularly as determined by principal components analyses (PCA), which is a descriptive rather than a discriminatory tool. Most variation detected by PCA was in size rather than shape. Despite this similarity in shape, species differ distinctly in their possession of specific characters, and we used these characters to separate them.

Analyses of variance (ANOVA), correlation matrices, and multivariate analyses were carried out using BMDP on the University of Kansas Academic Computing Services' IBM VM/CMS computer system. All data were log-transformed prior to carrying out these analyses.

Elevational and geographic distributions and the correlation of character states to these distributions were examined for all members of the *C. nigrescens* group.

Specimens used in our analyses are listed in the Specimens Examined section. These specimens are deposited in the following institutions: American

Museum of Natural History, New York (AMNH); Angelo State Natural History Collections, San Angelo, Texas (ASNHC); Escuela Nacional de Ciencias Biológicas, Mexico (ENCIB); Field Museum of Natural History, Chicago (FMNH); Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City (IBUNAM); Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica (INBio); University of Kansas Museum of Natural History, Lawrence (KU); Los Angeles County Museum, Los Angeles (LACM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of the High Plains, Fort Hays State University, Hays, Kansas (MHP); James Ford Bell Museum of Natural History, University of Minnesota, Minneapolis (MMNH); Museo Nacional de Costa Rica, San José (MNCR); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Royal Ontario Museum, Toronto (ROM); University of Iowa Museum of Natural History, Iowa City (SUI); Departamento de Biología, Universidad Autónoma Metropolitana Iztapalapa, Mexico (UAMI); University of Michigan Museum of Zoology, Ann Arbor (UMMZ); Universidad Nacional Autónoma de Honduras, Tegucigalpa (UNAH); and U.S. National Museum, Washington, D.C. (USNM).

## Sexual Variation

Male and female *Cryptotis* are difficult to tell apart, and few tests for sexual dimorphism within the genus have been carried out, at least in part because there are few good series of individuals of known sex. The two studies that have investigated sexual dimorphism in *Cryptotis* indicate that sexual differences in mensural variables are minor at most. Choate (1970) found only one of seven variables (length of maxillary tooth row) that he examined to be significantly different between the sexes in his morphometric analysis of *C. mexicana* from near Jalapa, Veracruz, Mexico. Only 1 of 19 variables differed significantly between males and females of *C. gracilis* in Costa Rica and Panama (Woodman, 1992); zygomatic plate length was significantly longer in females.

We tested for secondary sexual variation in *C. nigrescens* using our two largest series of sexed individuals. One included 17 males (14 crania, 16 skins) and 16 females (12 crania, 16 skins) from Monteverde, Costa Rica, and the other consisted of 13 males (13 crania, 9 skins) and 10 females

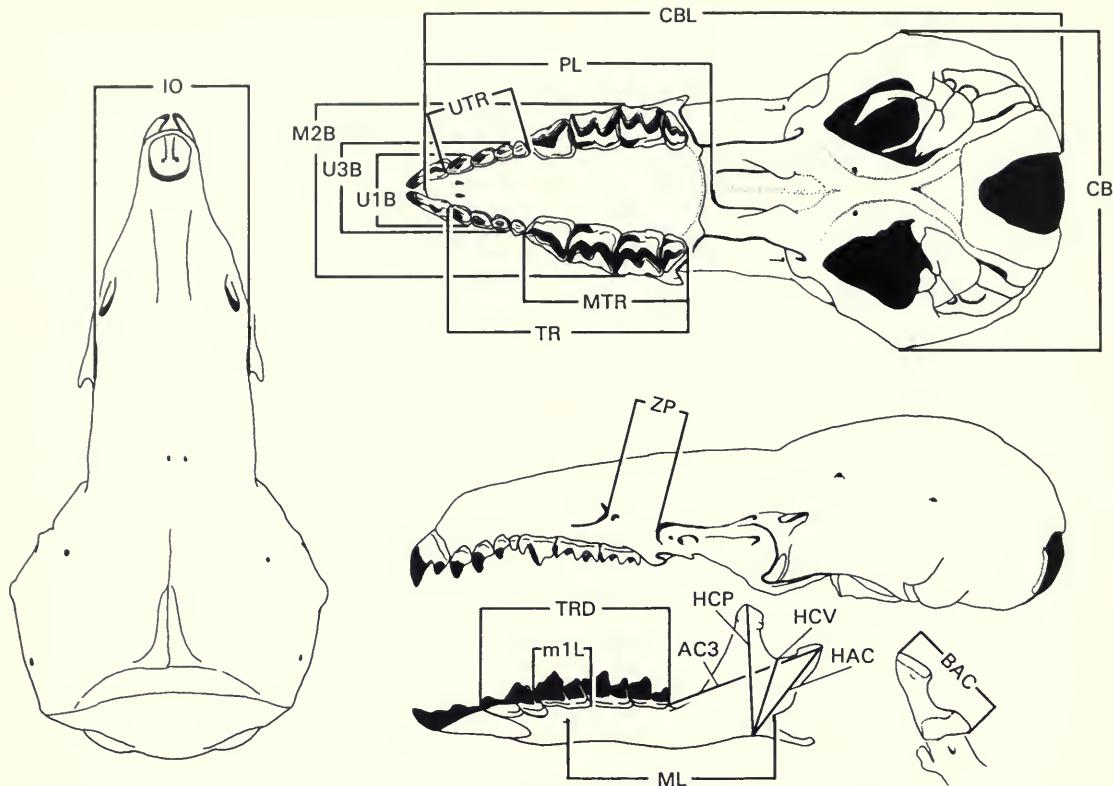


FIG. 1. Cranial and mandibular measurements used in this study. Abbreviations of variables are explained in the Methods section of text.

(10 crania, 8 skins) from near San Félix (including Cerro Bollo), Panama. A correlation matrix was calculated for 19 craniomandibular variables (CBL, CB, ZP, IO, U1B, M2B, PL, TR, UTR, MTR, WM1, ML, HCP, HAC, BAC, TRD, m1L, AC3, HAV). Because sample sizes were different for skin variables and for craniomandibular variables, skin measurements (HB, TL) were not included in the correlation matrix. Variables then were culled so that no two variables in the remaining data set had a correlation coefficient of 0.75 or greater. This yielded eight variables (CBL, ZP, UTR, MTR, WM1, HAC, BAC, HCV); all other variables correlated strongly with CBL, except HCV, which was strongly correlated with HAC. A two-way ANOVA was calculated for each of these eight craniomandibular variables and the two skin variables. Both sex and locality (Monteverde vs. San Félix) were tested as sources of variance to separate effects of sexual dimorphism and geographic variation. Statistical significance was determined using a Brown-Forsythe test for equality of means, which does not assume equality of the variances. Pro-

tected alpha values were not used despite a lack of independence among the variables tested, because protected values would have increased the likelihood of making Type II errors (i.e., incorrectly accepting no difference between males and females or between localities).

Only one variable, UTR ( $P = 0.0042$ ), exhibited a statistically significant difference between sexes, with females larger than males. In addition, CBL ( $P = 0.0566$ ) was close to being significantly different; again, females were larger than males. Five of the 10 variables (ZP, MTR, WM1, BAC, HCV) had  $P > 0.30$ , indicating no distinction between the sexes. The remaining three variables (HB, TL, HAC) had probabilities falling between 0.10 and 0.30, providing no clear evidence of whether a difference existed between males and females. Females averaged slightly larger than males for five measurements in the groups from both Monteverde (TL, CBL, ZP, UTR, HAC) and San Félix (CBL, UTR, MTR, HAC, m1L), although not for all the same variables. Males from Monteverde were larger than females for HB, and males from

San Félix were larger for HB and TL. However, actual differences between male and female means in both groups were small (table 1). If we use the differences, taken to four decimal places, between the male and female means for the eight craniomandibular variables, we find that they average 0.0470 (range = 0.0169–0.0892) for the specimens from San Félix and 0.0926 (range = 0.0107–0.4630) for specimens from Monteverde. Most are below our ability to measure accurately.

In contrast to the sex term, 9 of the 10 variables tested were significantly different between localities. Seven of these variables (HB, TL, CBL, UTR, WM1, HAC, BAC) had  $P < 0.001$ , and two (MTR, m1L) had  $P < 0.05$ . Only ZP showed no difference between the populations at Monteverde and San Félix ( $P = 0.3531$ ). For all variables, specimens from San Félix averaged larger than those from Monteverde. In fact, males from San Félix averaged larger than females from Monteverde for all variables except ZP, UTR, and m1L.

The interaction between sex and locality was not significant for any variables, and  $P < 0.30$  for only TL ( $P = 0.0734$ ), CBL ( $P = 0.0947$ ), and ZP ( $P = 0.2593$ ).

Body mass has been shown to be a good correlate of other estimators of size in some other small mammals (Iskjaer et al., 1989). Average weights of males and females from Monteverde were the same (table 1), giving no indication of sexual dimorphism. However, our use of body mass was hampered by the imprecision with which very small animals can be weighed in the field and small sample sizes available. Geographic variation could not be evaluated, because weights were not available for specimens from San Félix.

To test whether all craniomandibular variables together would show size differentiation between males and females, we ran PCAs separately for specimens from Monteverde and from San Félix using the original 19 craniomandibular variables and the same individuals as for the ANOVAs. Because all variables generally load heavily on factor axis 1 in a PCA, this axis provides a good estimator of overall size. Therefore, factor 1 scores should prove to be useful in determining any obvious patterns of size differentiation between the sexes. In the PCA of specimens from Monteverde, factor 1 estimates size and factor 2 is a shape score representing contrast between a combination of m1L and WM1 vs. the negatively weighted AC3 (table 2). A plot of factor 1 and factor 2 scores for these specimens (fig. 2) indicates nearly complete overlap of males and females on both the size and

shape axes. In the PCA of specimens from San Félix, factor 1 represents size and factor 2 is a contrast between shape of the articular condyle of the mandible (HCV and HAC) vs. a negatively weighted m1L (table 3). In the plot of factor 1 and factor 2 scores for these specimens (fig. 3), males and females exhibit complete overlap along the shape axis. Along the size axis, however, there is separation of the two sexes. Males range along the entire length of factor axis 1 but are more concentrated at the lower end of the scale. Females all cluster toward the upper end of the scale.

Our analysis of sexual variation in *C. nigrescens* shows no clear pattern of sexual dimorphism in size within this species. Although females generally averaged larger in most craniomandibular measurements in which there were differences between the sexes, males averaged larger in HB, especially among specimens from San Félix. The overlap between males and females for all measurements was great. Only two variables were significant or close to being significant when tested for differences between the sexes, and the statistical significance of those variables may have been a result of multiple comparison of dependent means. No other variables tested were clearly different. PCA indicated a tendency for male and female *C. nigrescens* from San Félix to separate out on size, but this was not the case for those from Monteverde, and the size range for males from San Félix overlapped completely that of females.

These results indicate that any sexual variation that exists is beyond our ability to measure accurately and precisely in these diminutive mammals. Differences between sexes were considerably less than differences between geographic localities, and they did not influence statistical tests among populations or contribute significantly to overall patterns of geographic variation in which we were interested. Possessing few sexed individuals from each locality, we could not partition our sample into tooth-wear classes (Rudd, 1955) and thus proportion out possible effects of age-related differences. However, because sexual variation did not inhibit our ability to detect geographic variation within *C. nigrescens*, we used males, females, and unsexed individuals in all subsequent analyses.

## Systematic Descriptions

In the following descriptions, species are arranged geographically, roughly from northwest to

TABLE 1. Selected measurements of male and female *C. nigrescens* from Monteverde, Costa Rica, and San Félix, Panama. Abbreviations of measurements are explained in the Methods section of text. The statistics presented are mean  $\pm$  standard deviation of the mean, and observed extremes. Number of individuals for each species is in parentheses.

	Monteverde		San Félix	
	Males	Females	Males	Females
HB	68 $\pm$ 5 60–76 (16)	67 $\pm$ 7 56–79 (16)	77 $\pm$ 3 72–83 (9)	74 $\pm$ 4 68–79 (8)
TL	28 $\pm$ 4 20–34 (16)	30 $\pm$ 2 27–33 (16)	34 $\pm$ 2 29–37 (9)	33 $\pm$ 2 30–36 (8)
CBL	17.9 $\pm$ 0.5 16.9–18.7 (14)	18.4 $\pm$ 0.5 17.7–19.3 (12)	19.2 $\pm$ 0.4 18.7–20.2 (13)	19.3 $\pm$ 0.4 18.3–19.8 (10)
CB	9.0 $\pm$ 0.2 8.7–9.4 (14)	9.0 $\pm$ 0.3 9.4–10.0 (12)	9.7 $\pm$ 0.2 9.4–10.3 (13)	9.7 $\pm$ 0.2 9.2–10.0 (10)
ZP	1.9 $\pm$ 0.2 1.6–2.2 (14)	2.0 $\pm$ 0.1 1.8–2.2 (12)	2.0 $\pm$ 0.2 1.5–2.5 (13)	2.0 $\pm$ 0.2 1.6–2.2 (10)
IO	4.2 $\pm$ 0.1 4.0–4.3 (14)	4.2 $\pm$ 0.2 4.0–4.7 (12)	4.6 $\pm$ 0.1 4.4–4.9 (13)	4.6 $\pm$ 0.2 4.3–4.8 (10)
U1B	2.3 $\pm$ 0.1 2.2–2.5 (14)	2.3 $\pm$ 0.1 2.2–2.5 (12)	2.6 $\pm$ 0.1 2.5–2.8 (13)	2.6 $\pm$ 0.1 2.5–2.7 (10)
M2B	5.3 $\pm$ 0.1 5.1–5.6 (14)	5.3 $\pm$ 0.2 4.9–5.6 (12)	5.7 $\pm$ 0.1 5.5–5.9 (13)	5.8 $\pm$ 0.1 5.5–6.0 (10)
PL	7.6 $\pm$ 0.2 7.2–7.9 (14)	7.9 $\pm$ 0.3 7.4–8.6 (12)	8.1 $\pm$ 0.2 7.8–8.3 (13)	8.3 $\pm$ 0.3 7.8–8.8 (10)
TR	6.8 $\pm$ 0.2 6.4–7.2 (14)	7.1 $\pm$ 0.2 6.7–7.3 (12)	7.4 $\pm$ 0.2 7.2–7.6 (13)	7.5 $\pm$ 0.3 6.9–7.8 (10)
UTR	2.3 $\pm$ 0.2 2.0–2.5 (14)	2.4 $\pm$ 0.1 2.3–2.5 (12)	2.4 $\pm$ 0.1 2.2–2.6 (13)	2.5 $\pm$ 0.1 2.4–2.6 (10)
MTR	5.2 $\pm$ 0.2 4.8–5.5 (14)	5.2 $\pm$ 0.2 4.8–5.6 (12)	5.3 $\pm$ 0.1 5.2–5.5 (13)	5.4 $\pm$ 0.2 4.9–5.7 (10)
WM1	1.7 $\pm$ 0.1 1.5–1.8 (14)	1.7 $\pm$ 0.1 1.6–1.8 (12)	1.8 $\pm$ 0.05 1.7–1.9 (13)	1.8 $\pm$ 0.1 1.7–1.9 (10)
ML	6.1 $\pm$ 0.2 5.7–6.5 (14)	6.3 $\pm$ 0.2 5.9–6.6 (12)	6.4 $\pm$ 0.3 6.0–6.9 (13)	6.5 $\pm$ 0.2 6.1–6.9 (10)
HCP	4.3 $\pm$ 0.2 4.0–4.6 (14)	4.4 $\pm$ 0.2 4.1–4.7 (12)	4.7 $\pm$ 0.1 4.6–5.0 (13)	4.8 $\pm$ 0.1 4.6–5.0 (10)
HCV	2.6 $\pm$ 0.1 2.4–2.8 (14)	2.7 $\pm$ 0.1 2.5–2.9 (12)	2.8 $\pm$ 0.1 2.6–3.0 (13)	2.9 $\pm$ 0.1 2.8–3.0 (10)
HAC	3.6 $\pm$ 0.2 3.3–3.9 (14)	3.7 $\pm$ 0.2 3.4–4.0 (12)	3.8 $\pm$ 0.2 3.5–4.1 (13)	3.9 $\pm$ 0.1 3.7–4.0 (10)

TABLE 1. *Continued.*

	Monteverde		San Félix	
	Males	Females	Males	Females
BAC	2.9 ± 0.1 2.7–3.1 (14)	2.9 ± 0.1 2.7–3.1 (12)	3.0 ± 0.1 2.9–3.2 (13)	3.0 ± 0.1 2.9–3.2 (10)
AC3	4.4 ± 0.2 4.1–4.7 (14)	4.5 ± 0.2 4.2–4.8 (12)	4.6 ± 0.2 4.4–5.1 (13)	4.7 ± 0.05 4.7–4.8 (10)
TRD	5.4 ± 0.2 5.1–5.6 (14)	5.5 ± 0.2 5.2–5.8 (12)	5.8 ± 0.1 5.7–6.2 (13)	5.9 ± 0.2 5.3–6.2 (10)
m1L	1.7 ± 0.1 1.6–1.8 (14)	1.7 ± 0.1 1.6–1.8 (12)	1.7 ± 0.1 1.6–1.9 (13)	1.8 ± 0.1 1.6–1.9 (10)
Weight (g)	6 ± 1 4–8 (13)	6 ± 1 5–7 (9)	—	—

southeast. Accounts are not provided for *C. hondurensis* or *C. magna*, although there is evidence that these two species may be included within the *C. nigrescens* group (Woodman, 1992). However, comparisons of these two species are made with the species described below.

#### *Cryptotis mayensis* (Merriam, 1901)

(fig. 4)

*Blarina mayensis* C. H. Merriam, 29 November 1901,  
Proc. Washington Acad. Sci. 3:559.

TABLE 2. Factor loadings from PCA of male and female *C. nigrescens* from Monteverde, Costa Rica. Abbreviations of measurements are explained in the Methods section of the text.

Variable	Factor 1	Factor 2
CBL	0.875	-0.179
TR	0.860	0.221
PL	0.857	-0.090
HCP	0.824	-0.260
ML	0.786	-0.175
TRD	0.755	0.485
U1B	0.728	0.007
HAC	0.708	-0.284
IO	0.692	0.102
BAC	0.667	-0.243
HCV	0.663	-0.390
M2B	0.658	0.440
UTR	0.652	0.160
MTR	0.642	0.392
AC3	0.606	-0.589
CB	0.596	-0.218
ZP	0.539	-0.283
m1L	0.535	0.584
WM1	0.445	0.582

*Cryptotis mayensis*: G. S. Miller, Jr., 31 December 1912, Bull. U.S. Natl. Mus. 79:26; R. T. Hatt, 18 August 1938, J. Mamm. 19:334; P. Hershkovitz, 10 July 1951, Fieldiana Zool. 31:522; R. T. Hatt et al., March 1953, Cranbrook Inst. Sci. Bull. 33:59; E. R. Hall and K. R. Kelson, 31 March 1959, The Mammals of North America 1:61; T. Alvarez and A. Martinez G., 4 August 1967, Southwest. Nat. 12: 205; R. L. Peterson, 26 November 1968, J. Mamm. 49:796.

*Blarina mexicana*: G. F. Gaumer, 1917, Monografía de los mamíferos de Yucatán, p. 249 (part).

*Cryptotis micrura*: A. Murie, 15 July 1935, Misc. Publ. Mus. Zool., Univ. Michigan 26:17 (part); E. R. Hall

TABLE 3. Factor loadings from PCA of male and female *C. nigrescens* from the vicinity of San Félix, Panama.

Variable	Factor 1	Factor 2
TRD	0.901	-0.291
MTR	0.879	-0.167
CBL	0.872	-0.278
TR	0.836	-0.051
PL	0.817	0.117
HCP	0.738	0.474
IO	0.716	0.088
BAC	0.713	0.379
CB	0.708	-0.248
ML	0.700	-0.417
M2B	0.682	0.176
AC3	0.570	-0.032
HCV	0.566	0.634
U1B	0.527	0.324
ZP	0.496	-0.219
UTR	0.459	-0.123
HAC	0.449	0.631
WM1	0.443	-0.290
m1L	0.340	-0.703

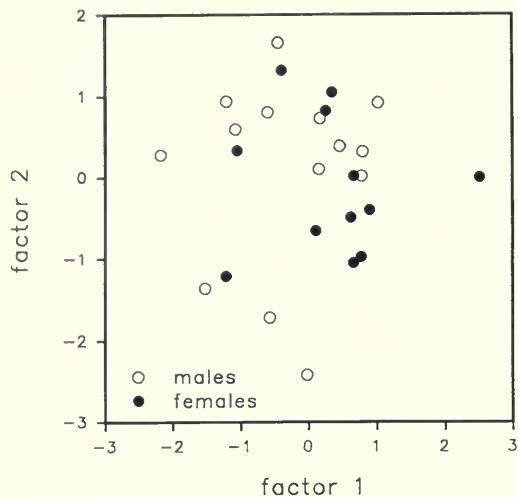


FIG. 2. Plot of PCA factor 1 and factor 2 scores for males and females of *C. nigrescens* from Monteverde, Costa Rica.

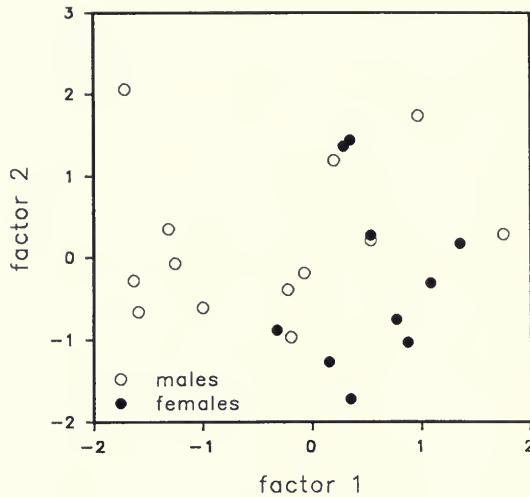


FIG. 3. Plot of PCA factor 1 and factor 2 scores for males and females of *C. nigrescens* from the vicinity of San Félix, Panama.

and K. R. Kelson, 31 March 1959, The Mammals of North America 1:62 (part).

*Cryptotis nigrescens mayensis*: J. R. Choate, 30 December 1970, Univ. Kansas Publ. Mus. Nat. Hist. 19:275; E. R. Hall, 3 April 1981, The Mammals of North America 1:63; R. C. Dowler and M. D. Engstrom, 15 December 1988, Ann. Carnegie Mus. 57: 160.

**HOLOTYPE**—Skin and skull of subadult female, U.S. National Museum of Natural History no. 108087, obtained by E. W. Nelson and E. A. Goldman (collector number 14495) 5 February 1901 from Mexico, Yucatán, Chichén Itzá.

**DISTRIBUTION**—Known primarily from below 100 m on the Yucatan Peninsula of Mexico and adjacent Belize and Guatemala (fig. 5). Also known from remains isolated from owl pellets collected in a cave at 650 m, in the Cañon del Zopilote, Guerrero, Mexico.

**DESCRIPTION**—A medium-sized *Cryptotis*, HB averaging 69 (table 4); tail short, averaging 41% ( $\pm 5\%$ ,  $n = 11$ ) of HB; dorsal hairs about 3 mm long, ranging from about 2 to 4 mm, three-banded; dorsum often has mottled, salt and pepper appearance; dorsal pelage variable: Pale Ecru-Drab and Drab, Light Drab, Light Mouse Gray to Deep Mouse Gray, Pale Mouse Gray or Mouse Gray with touches of Olive Brown; lateral pelage from Smoke Gray to Mouse Gray; venter slightly paler than dorsum, may include one or more of the following: Pale Olive Gray, Light Olive Gray, Light Grayish Olive, Pale Mouse Gray to Light Mouse Gray.

Rostrum narrow and of normal length (PL/CBL =  $43.4\% \pm 1.2$ ,  $n = 10$ ); interorbital area moderately wide; usually only one dorsal foramen (81%,  $n = 65$ ) located on either the right or left frontal, small to medium in size; a well-developed foramen leading to a ventral extension of the sinus canal typically present posterior to the dorsal articular facet on one (8%,  $n = 62$ ) or both (86%) sides of the skull; normally no foramen dorsal to dorsal articular facet (93%,  $n = 61$ ); anterior process of the petromastoid low and very narrow (fig. 18A); paroccipital process prominent; zygomatic plate broad in proportion to CBL ( $11.8\% \pm 0.7$ ,  $n = 10$ ) and PL ( $27.8\% \pm 1.6$ ,  $n = 72$ ); anterior border of zygomatic plate from parastyle/mesostyle valley to mesostyle of M1, posterior border from metastyle of M2 to middle of M3, and from posterior one-third of base of maxillary process to posterior to maxillary process; palate long and narrow; upper tooth row crowded; unicuspids massive; U4 normally displaced medially, so that U3 and P4 in contact or nearly so; U4 not visible in lateral view of skull; lateral view of U3 also sometimes partially obstructed by P4; posterior borders of P4, M1, and M2 unrecessed or only very slightly recessed; M3 with well-developed paracrista and paracone, reduced precentrocrista, poorly developed and normally uncolored mesostyle and protocone, and hypocone absent or vestigial and incorporated into the posterior cingulum; dentition bulbous.

Mandible large; horizontal ramus deep; coronoid process high (HCP/ML =  $84.3\% \pm 3.3$ ,  $n =$

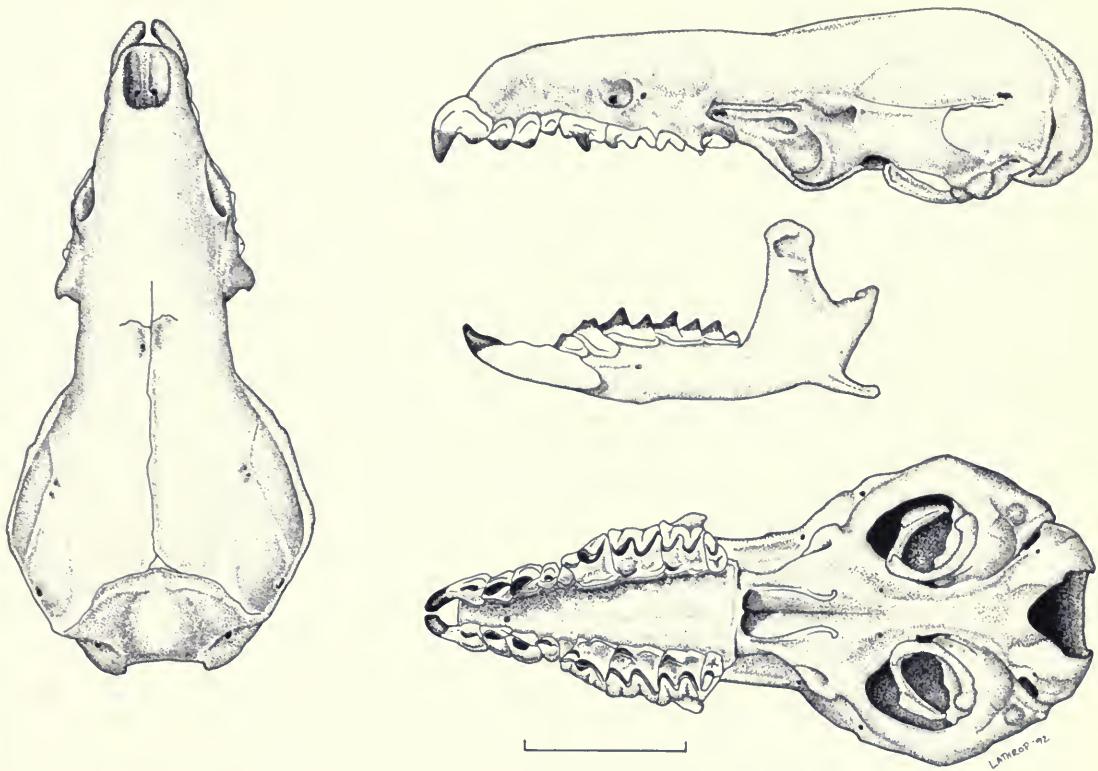


FIG. 4. Dorsal, ventral, and lateral views of the skull and lateral view of the skull and mandible of *C. mayensis* (ASNHC 6071). Scale bar = 5 mm.

21) and broad, joins mandible at steep angle; viewed posteriorly, horizontal and vertical branches of articular condyle short and broad; lower sigmoid notch very shallow, not extending beneath ventral border of articular process; posterior border of lower incisor extends nearly to posterior border of cingulum of p4; lower dentition wide; only hypoconid in talonid of m3.

**COMPARISONS**—*Cryptotis mayensis* has the palest pelage of any member of the *C. nigrescens* group, appearing medium gray (often speckled with patches of white) rather than dark brown to black.

***Cryptotis magna***—*C. mayensis* is much smaller (HB averaging 69 vs. 86; table 4) and has much paler pelage; much shorter tail (averaging 41% of HB vs. 53%); skull much smaller in all dimensions, but zygomatic plate relatively broader (averaging 11.8% of CBL vs. 10.1%  $\pm$  0.6); usually only one dorsal foramen; well-developed foramen posterior to dorsal articular facet (foramen present but always vestigial in *C. magna*); rarely possesses foramina dorsal to dorsal articular facet; no entoconid in talonid of m3 (vestigial entoconid present in *C. magna*).

***Cryptotis hondurensis***—*C. mayensis* is much larger (HB averaging 69 vs. 61  $\pm$  5; table 4) and has much paler pelage; shorter tail (averaging 41% vs. 46%); M3 less complex, lacking metacone; dentition bulbous; coronoid process of mandible much higher and broader.

**REMARKS**—The pelage of *Cryptotis mayensis* is paler than in any other member of the genus, including *C. parva*, from which the coloration differs in being more gray and less olive. The overall appearance of *C. mayensis* is a medium brownish gray. Close inspection of the dorsal pelage of *C. mayensis* reveals that the individual hairs are three-banded. The proximal one-half to three-quarters of the hairs is a medium gray, followed by a narrow band of light gray. The distal tip (about one-eighth of the total length) of the hair is brownish gray. The transition between bands is not sharp, with the colors instead tending to grade into each other. The great extent of lighter, basal coloration in the hairs of this taxon probably accounts for its overall paler appearance and greater reflectance.

Goldman (1951) described the northern Yucatan habitat around Chichén Itzá, from which the

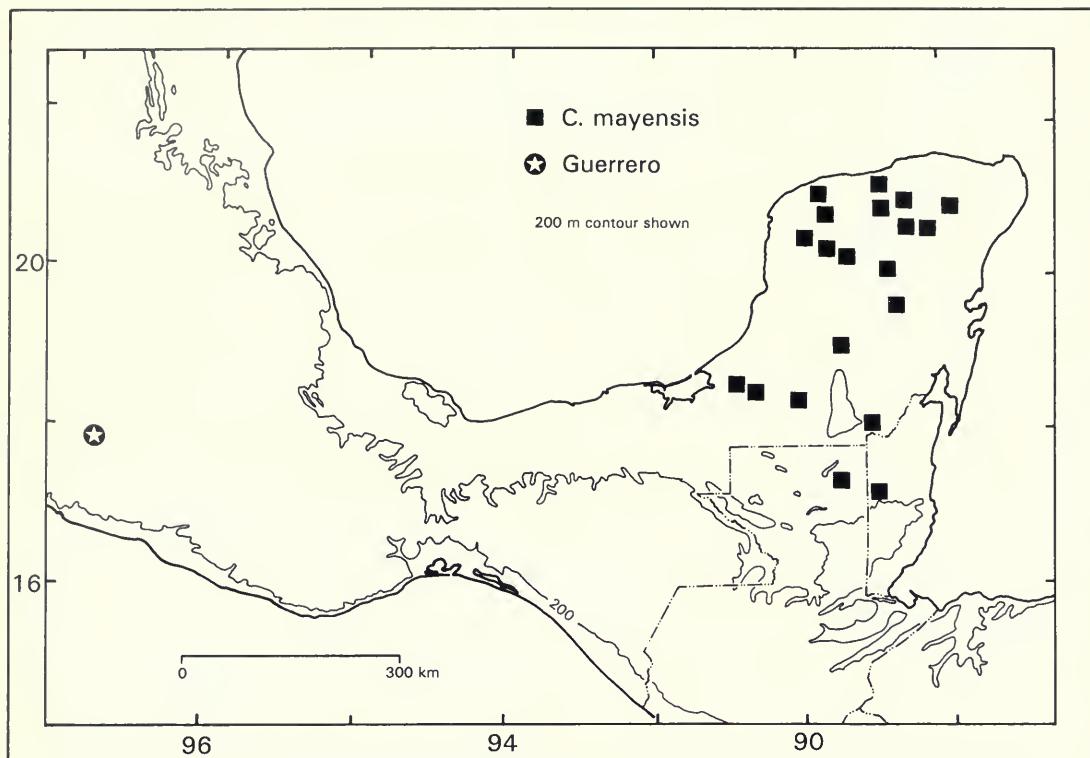


FIG. 5. Map of southern Mexico, Belize, and Guatemala showing the distribution of *C. mayensis*.

holotype of *C. mayensis* was collected, as stunted tropical forest about 25–40 ft high with dense, brushy undergrowth. He noted that the weather is highly seasonal, with a long, hot, dry season from about December to June and a rainy season marked by torrential afternoon showers. Dowler and Engstrom (1988) reported a specimen from 7.5 km W Escárcega, Campeche, as having been trapped in mature, transitional deciduous-evergreen forest. In the same area they also collected *Heteromys gaumeri*, *Ototylomys phyllotis*, *Peromyscus yucatanicus*, and *Oryzomys melanotis*. Two *C. mayensis* from 60 km SE of Dzibalchén, Campeche, were taken in pitfalls set in transitional deciduous-evergreen forest dominated by escobal palms (*Cryosophila*) and *Sabal* palms (M. D. Engstrom, in litt.). Alvarez and Martinez (1967) captured a *C. mayensis* along a road in tropical rain forest opposite a cornfield, 2 km SE Laguna Chickankanaab, Quintana Roo.

Few reproductive data are available for *C. mayensis*, and no pregnant or lactating females have been recorded. Males captured on 4 June, 24 June, and 19 August showed no indications of having lateral glands. When present, these paired glan-

dular areas lack long guard hairs and underfur but have a sparse covering of short, fine hairs (Woodman & Timm, submitted). Both males and females possess lateral glands, but in females they are much smaller and more difficult to see (Murariu, 1976; Bee et al., 1980). It is likely that these glands serve a function in sexual communication. Eadie (1938) found that the lateral glands of male *Blarina* showed increased activity with enlargement of the testes.

*Cryptotis mayensis* is rarely collected, and there are few complete specimens in museum collections. However, it is unlikely that this shrew is truly rare, because remains from owl pellets are abundant. Of 122 specimens examined in our study, 76 came from owl pellets, 33 are from archaeological contexts, and 13 are standard museum specimens.

*Cryptotis mayensis* is distinctive in being the only member of the genus restricted to lowland areas. On the Yucatan Peninsula the species is not known to occur above 100 m. The only specimens of *C. mayensis* from outside of the Yucatan Peninsula are crania and unassociated mandibles collected by William López-Forment C. in 1969 from below a barn owl (*Tyto alba*) roost in Macultzingo

Cave [Cueva del Cañon de Zopilote], located at 650 m in the Cañon de Zopilote, Guerrero, Mexico (Choate, 1970). The precise locality and habitat where the shrews were captured by owls is unknown, and subsequent work in Macuiltzingo Cave has not produced additional specimens (López-Forment & Urbano, 1977; W. López-Forment C., pers. comm.), suggesting a change in feeding patterns by the owls or local extinction of the population of shrews upon which they were feeding. When one of us (Woodman) visited the cave with W. López-Forment C. in August 1991, no owls were occupying the cave, and there was no evidence of any recent use of the cave by owls. Despite repeated collecting in the region surrounding the cave (Choate, 1970; W. López-Forment C., pers. comm.; fieldwork by Woodman in 1991), no additional specimens of these shrews have been obtained.

The presence of shrews identifiable as *C. mayensis* in Guerrero presents an interesting biogeographical problem. These shrews are from an area that clearly is isolated geographically from the Yucatan Peninsula and is climatically and vegetationally distinct. Choate (1970) noted the great distance (> 950 km) and extensive biogeographical barriers between Zopilote Canyon and the nearest known locality of *C. mayensis* on the Yucatan Peninsula and suggested that the specimens from Zopilote Canyon eventually might prove to be subspecifically distinct. All known specimens from Guerrero are mandibles and incomplete skulls, making comparisons with other taxa, including *C. mayensis*, difficult.

Because the specimens from Guerrero were from far outside the range of all other populations on the Yucatan Peninsula, and because of the geographical barriers and habitat differences between the two areas, we considered that specimens from Guerrero might prove to be either misidentified or an undescribed species. The fragmentary nature of the specimens from Guerrero limited the measurements that could be taken from them and did not yield characters useful for separating them from *C. mayensis* on the Yucatan Peninsula. We carried out PCAs and discriminant function analyses in order to test the overall similarity of the two groups of specimens. Crania and mandibles were tested separately, because these elements are disassociated in all known specimens from Guerrero. Analyses of crania included six variables (ZP, IO, M2B, PL, MTR, WM1) measured on 20 *C. mayensis* from the Yucatan Peninsula, 16 *C. merriami*, and 20 specimens from Guerrero. Analyses carried

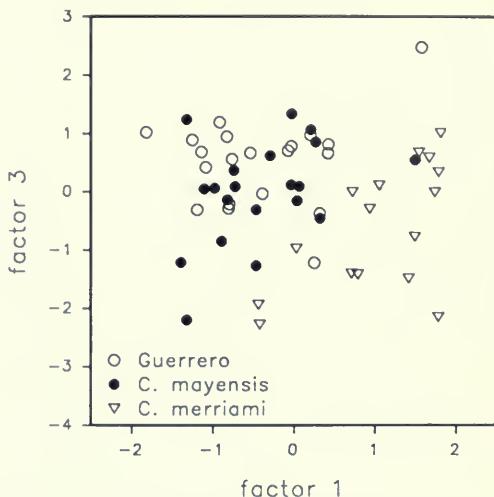


FIG. 6. Plot of specimens of *C. mayensis* from Guerrero and the Yucatan Peninsula and *C. merriami* on factor axes 1 and 3 from PCA of cranial variables.

out on mandibles utilized eight variables (ML, HCP, HCV, HAC, BAC, TRD, m1L, AC3) from 20 *C. mayensis*, 24 *C. merriami*, and six mandibles from Guerrero. Specimens of *C. merriami* were included to determine whether or not the variables used were useful for distinguishing groups.

PCAs indicated wide overlap of *C. mayensis* from the Yucatan with specimens from Guerrero. In the PCA of crania, all variables except ZP loaded out heavily on factor 1, providing a measure of overall size of the specimens (table 5). Factor 3 was a shape axis, providing a contrast between PL and M2B. Factor 2 from this analysis represented a contrast between a very heavily weighted ZP and a slightly negatively weighted WM1; it did not aid in separating any groups. In a plot of factor scores (fig. 6), *C. mayensis* and specimens from Guerrero are essentially indistinguishable. *Cryptotis mayensis* and *C. merriami* are separated by a combination of size and shape. *Cryptotis merriami* tends to be larger cranially than *C. mayensis*, and, at any given size, *C. mayensis* has a longer but narrower palate than *C. merriami*.

In the PCA carried out using mandibles, factor 1 is a size axis and factor 2 is a contrast between a combination of variables representing length of the mandible (m1L, TRD, ML) and HCP (table 6). A plot of specimens on factor 1 and factor 2 (fig. 7) shows *C. mayensis* from the Yucatan Peninsula and specimens from Guerrero again intermixed. In contrast to the PCA using cranial variables, *C. merriami* and *C. mayensis* do not separate out on the size axis but can be discriminated by

TABLE 4. Selected measurements of members of the *C. nigrescens* group. Abbreviations of measurements are explained in the Methods section of text. The statistics presented are mean  $\pm$  standard deviation of the mean, and observed extremes. Number of individuals for each species is in parentheses.

	<i>C. mayensis</i>	<i>C. magna</i>	<i>C. merriami</i>	<i>C. hondurensis</i> (holotype and 2 paratypes)	<i>C. nigrescens</i>	<i>C. mera</i>	<i>C. colombiana</i> (holotype)
HB	69 $\pm$ 8 61–90 (11)	86 $\pm$ 6 70–100 (47)	69 $\pm$ 4 60–77 (23)	55, 63, 64	68 $\pm$ 7 55–83 (70)	69 $\pm$ 2 67–73 (6)	76
TL	28 $\pm$ 3 24–33 (11)	46 $\pm$ 4 34–53 (47)	29 $\pm$ 4 22–38 (23)	29, 27, 27	29 $\pm$ 4 19–37 (70)	27 $\pm$ 2 24–31 (6)	27
TL as % of HB	41 $\pm$ 5 31–49 (11)	54 $\pm$ 6 34–64 (47)	43 $\pm$ 6 32–55 (23)	53, 43, 42	43 $\pm$ 5 28–53 (70)	39 $\pm$ 4 34–46 (6)	36
CBL	19.0 $\pm$ 0.4 18.2–19.6 (10)	22.8 $\pm$ 0.4 21.9–23.4 (17)	19.4 $\pm$ 0.4 18.7–20.0 (16)	19.2, —, —	18.6 $\pm$ 0.7 16.9–20.2 (70)	18.3 $\pm$ 0.4 17.7–18.7 (6)	19.9
CB	9.2 $\pm$ 0.3 8.8–9.8 (10)	11.6 $\pm$ 0.2 11.2–12.3 (17)	9.6 $\pm$ 0.2 9.2–10.0 (18)	9.2, —, —	9.2 $\pm$ 0.4 8.0–10.3 (70)	9.4 $\pm$ 0.3 9.1–9.8 (6)	10.0
ZP	2.3 $\pm$ 0.1 2.0–2.5 (21)	2.3 $\pm$ 0.1 2.1–2.6 (17)	2.3 $\pm$ 0.2 2.0–2.6 (21)	2.2, 2.0, 2.1	2.0 $\pm$ 0.2 1.5–2.5 (70)	2.0 $\pm$ 0.1 1.9–2.2 (6)	2.0
IO	4.4 $\pm$ 0.2 4.1–4.8 (21)	5.6 $\pm$ 0.1 5.4–5.8 (17)	4.7 $\pm$ 0.1 4.4–4.9 (21)	4.3, 4.5, —	4.4 $\pm$ 0.2 3.9–4.9 (70)	4.5 $\pm$ 0.2 4.3–4.7 (6)	4.9
U1B	2.6 $\pm$ 0.1 2.2–2.7 (21)	3.2 $\pm$ 0.1 3.0–3.4 (17)	2.6 $\pm$ 0.2 2.1–2.8 (21)	2.4, 2.4, —	2.4 $\pm$ 0.2 2.1–2.8 (70)	2.5 $\pm$ 0.1 2.4–2.6 (6)	2.6
U3B	3.0 $\pm$ 0.1 2.8–3.3 (21)	3.7 $\pm$ 0.2 3.5–3.9 (17)	3.0 $\pm$ 0.2 2.7–3.1 (6)	2.9, 3.0, —	2.8 $\pm$ 0.2 2.4–3.2 (70)	2.9 $\pm$ 0.1 2.7–3.0 (6)	3.2
M2B	5.5 $\pm$ 0.1 5.2–5.7 (21)	6.8 $\pm$ 0.1 6.5–7.0 (17)	5.8 $\pm$ 0.2 5.2–6.2 (21)	5.4, 5.4, —	5.5 $\pm$ 0.3 4.9–6.0 (70)	5.6 $\pm$ 0.1 5.5–5.8 (6)	6.3
PL	8.3 $\pm$ 0.3 7.8–9.0 (21)	10.1 $\pm$ 0.3 9.6–10.8 (17)	8.4 $\pm$ 0.3 7.9–8.9 (21)	8.4, 7.8, —	7.9 $\pm$ 0.3 7.2–8.8 (70)	7.8 $\pm$ 0.1 7.6–7.8 (6)	8.8
TR	7.3 $\pm$ 0.2 6.9–7.8 (21)	9.1 $\pm$ 0.2 8.8–9.3 (17)	7.4 $\pm$ 0.2 6.8–7.7 (21)	7.1, 7.1, 7.1	7.1 $\pm$ 0.3 6.4–7.8 (70)	7.1 $\pm$ 0.1 6.9–7.2 (6)	7.7
UTR	2.7 $\pm$ 0.2 2.1–3.1 (21)	3.2 $\pm$ 0.1 3.1–3.4 (17)	2.5 $\pm$ 0.1 2.2–2.7 (21)	2.6, 2.4, 2.4	2.4 $\pm$ 0.1 2.0–2.6 (70)	2.4 $\pm$ 0.1 2.3–2.5 (6)	2.5
MTR	5.0 $\pm$ 0.1 4.8–5.3 (21)	5.1 $\pm$ 0.6 5.1–5.2 (17)	5.2 $\pm$ 0.2 5.0–5.5 (17)	5.1, 5.1, 5.2	5.2 $\pm$ 0.2 4.7–5.7 (70)	5.1 $\pm$ 0.05 5.1–5.2 (6)	5.8
WM1	1.7 $\pm$ 0.0 1.7–1.8 (21)	1.8 $\pm$ 0.1 1.7–1.9 (17)	1.9 $\pm$ 0.1 1.7–2.0 (21)	1.7, 1.7, 1.9	1.8 $\pm$ 0.1 1.5–1.9 (70)	1.8 $\pm$ 0.05 1.8–1.9 (6)	1.8
ML	6.2 $\pm$ 0.2 5.8–6.8 (24)	7.3 $\pm$ 0.2 6.8–7.6 (17)	6.5 $\pm$ 0.3 6.0–7.2 (21)	6.1, 5.8, 6.3	6.2 $\pm$ 0.3 5.5–6.9 (70)	5.9 $\pm$ 0.4 5.2–6.2 (6)	6.9

TABLE 4. *Continued.*

	<i>C. mayensis</i>	<i>C. magna</i>	<i>C. merriami</i>	<i>C. hondurensis</i> (holotype and 2 paratypes)	<i>C. nigrescens</i>	<i>C. mera</i>	<i>C. colombiana</i> (holotype)
HCP	5.3 ± 0.3 4.8–5.7 (24)	6.1 ± 0.2 5.7–6.3 (17)	5.0 ± 0.2 4.6–5.3 (21)	4.8, 4.4, 4.6	4.5 ± 0.3 4.0–5.0 (70)	4.5 ± 0.1 4.3–4.6 (6)	4.8
HCV	2.9 ± 0.1 2.7–3.2 (24)	3.4 ± 0.1 3.2–3.7 (17)	2.9 ± 0.2 2.6–3.3 (21)	2.7, 2.7, 2.7	2.7 ± 0.2 2.3–3.0 (70)	2.7 ± 0.1 2.6–2.8 (6)	2.9
HAC	3.9 ± 0.2 3.4–4.4 (24)	4.6 ± 0.1 4.4–4.8 (17)	3.8 ± 0.2 3.5–4.3 (21)	3.6, 3.6, 3.8	3.7 ± 0.2 3.3–4.1 (70)	3.7 ± 0.1 3.6–3.8 (6)	4.1
BAC	3.1 ± 0.1 2.8–3.3 (24)	3.6 ± 0.1 3.4–3.8 (17)	3.0 ± 0.1 2.6–3.2 (21)	3.0, 2.8, 2.8	2.9 ± 0.1 2.6–3.2 (70)	3.0 ± 0.1 2.9–3.1 (6)	3.1
AC3	4.8 ± 0.2 4.4–5.3 (24)	5.8 ± 0.2 5.3–6.3 (17)	4.6 ± 0.2 4.3–4.9 (21)	4.3, 4.3, 4.4	4.5 ± 0.2 3.8–5.1 (70)	4.4 ± 0.1 4.3–4.6 (6)	4.9
TRD	5.5 ± 0.2 5.3–5.8 (24)	6.9 ± 0.1 6.6–7.1 (17)	5.7 ± 0.2 5.3–5.9 (21)	5.5, 5.3, 5.7	5.6 ± 0.3 5.1–6.2 (70)	5.5 ± 0.1 5.4–5.7 (6)	6.0
m1L	1.7 ± 0.1 1.6–1.9 (24)	2.2 ± 0.1 2.1–2.4 (17)	1.8 ± 0.1 1.7–1.9 (21)	1.7, 1.7, 1.7	1.7 ± 0.1 1.6–1.9 (70)	1.8 ± 0.1 1.7–1.8 (6)	1.9

factor 2 scores. *Cryptotis merriami* has a relatively longer mandible and tooth row and a shorter coronoid process than *C. mayensis* and the specimens from Guerrero.

Discriminant function analysis of crania failed to distinguish effectively among the three groups of shrews. This analysis utilized a three-variable model (WM1, M2B, PL), which correctly identified fewer than 70% of specimens using a jack-knifed classification. A plot of specimens on canonical axes 1 and 2 (fig. 8) shows some distinction between *C. merriami* and the other two groups, but there is broad overlap between *C. mayensis* and the specimens from Guerrero. The pattern of linear groupings in this plot is due to one variable, WM1, which loaded out equally on each axis and for which there were only five states. These qualities made it act as a discrete variable rather than as a continuous variable. However, this does not affect the validity of the analysis nor the conclusion that *C. mayensis* from the Yucatan Peninsula and from Guerrero are difficult to distinguish.

The discriminant function analysis of mandibles utilized four variables (ML, HCP, HAC, BAC), which correctly classified 96% of *C. merriami*, 80% of *C. mayensis* from the Yucatan, and all of the

specimens from Guerrero. Intermixing between the two described taxa was minimal; only one *C. merriami* and one *C. mayensis* were incorrectly identified as the other taxon. However, three *C. mayensis* were misclassified as belonging to the group of specimens from Guerrero. A plot of specimens on canonical axes 1 and 2 shows clustering of individuals belonging to each of the three groups but not complete separation among groups (fig. 9). *Cryptotis merriami* can be distinguished from the other two groups along axis 1, whereas *C. mayensis* and the specimens from Guerrero cluster separately along axis 2.

Although there is some indication that *C. may-*

TABLE 5. Factor loadings from PCA of cranial variables of *C. mayensis* from the Yucatan Peninsula and Guerrero and *C. merriami*.

Variable	Factor 1	Factor 2	Factor 3
MTR	0.892	-0.099	0.096
M2B	0.869	0.047	-0.311
WM1	0.839	-0.233	-0.162
IO	0.828	0.003	-0.180
PL	0.681	0.071	0.708
ZP	0.198	0.970	-0.065

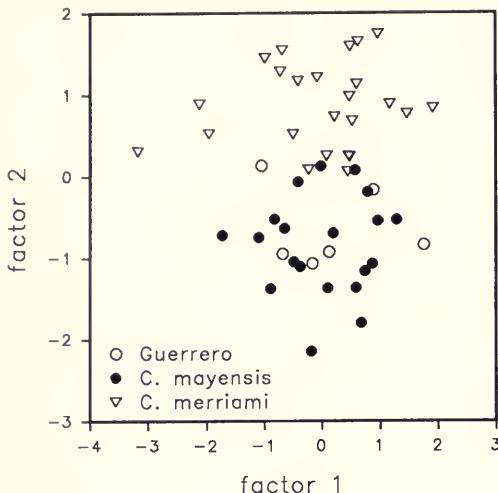


FIG. 7. Plot of specimens of *C. mayensis* from Guerrero and the Yucatan Peninsula and *C. merriami* on factor axes 1 and 2 from PCA of mandibular variables.

*ensis* and the shrews from Guerrero exhibit some differentiation, they are very similar, and at this time it seems best to refer the specimens from Guerrero to *C. mayensis*. We do this tentatively, however, and we believe that once more complete specimens are available the shrews from Guerrero will prove to be specifically distinct from *C. mayensis*. Alternatively, the shrews from Guerrero may represent a disjunct population of *C. mayensis*. This is supported by another species found with the shrews in the owl pellets from Macuiltzingo Cave, *Ototylomys phyllotis*, which otherwise is unknown north of the Isthmus of Tehuantepec. The specimens from Guerrero are indistinguishable from *O. p. phyllotis* from the Yucatan Peninsula, which in turn are easy to separate from *O. p. connectens* in Chiapas (M. D. Engstrom, in litt.).

Because of possible geographic variation, and because of their fragmentary nature, specimens

TABLE 6. Factor loadings from PCA of mandibular variables of *C. mayensis* from the Yucatan Peninsula and Guerrero and *C. merriami*.

Variable	Factor 1	Factor 2
HAC	0.873	-0.265
HCV	0.817	-0.005
BAC	0.814	-0.144
AC3	0.723	-0.290
HCP	0.701	-0.529
ML	0.672	0.560
TRD	0.383	0.813
m1L	0.285	0.858

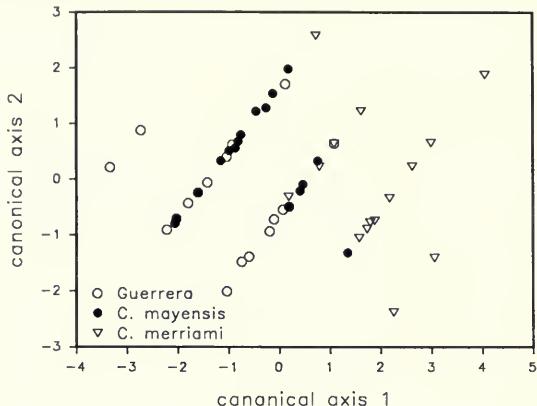


FIG. 8. Plot of specimens of *C. mayensis* from Guerrero and the Yucatan Peninsula and *C. merriami* on canonical axes 1 and 2 from discriminant function analysis of cranial variables.

from Guerrero were not included with other *C. mayensis* in calculations of univariate statistics or in other tests involving this taxon.

One specimen from Guerrero (IBUNAM 11039) has an auxiliary unicuspis (RU5 or a second RU4) in the upper right unicuspis tooth row. Supernumerary unicuspids previously have been reported for *Blarina* (Choate, 1968), but this appears to be a fairly rare dental abnormality in soricids. It is much more common for individuals to lack unicuspids (Choate, 1968, 1970).

#### *Cryptotis merriami* Choate, 1970 (fig. 10)

*Cryptotis nigrescens merriami* J. R. Choate, 30 December 1970, Univ. Kansas Publ. Mus. Nat. Hist. 19:277; E. R. Hall, 3 April 1981, The Mammals of North America 1:63.

*Cryptotis nigrescens*: G. G. Goodwin, 29 May 1942, Bull. Amer. Mus. Nat. Hist. 79:117; W. H. Burt and R. A. Stirton, 22 September 1961, Misc. Publ. Mus. Zool., Univ. Michigan 117:21.

*Cryptotis parva orophila*: J. R. Choate, 30 December 1970, Univ. Kansas Publ. Mus. Nat. Hist. 19:262 (part); E. R. Hall, 3 April 1981, The Mammals of North America 1:61 (part).

*Cryptotis nigrescens nigrescens*: J. R. Choate, 30 December 1970, Univ. Kansas Publ. Mus. Nat. Hist. 19:279 (part); E. R. Hall, 3 April 1981, The Mammals of North America 1:63 (part).

**HOLOTYPE**—Skin and skull of adult female, U.S. National Museum of Natural History no. 77050, obtained by E. W. Nelson and E. A. Goldman (collector number 8846) 21 December 1895 from

Guatemala, Huehuetenango, Jacaltenango, 5400 ft.

**DISTRIBUTION**—*Cryptotis merriami* occurs in the highlands of Chiapas, Guatemala, Honduras, El Salvador, and northern Nicaragua (fig. 11), with a disjunct population in the Tilarán Highlands of Costa Rica (fig. 14). Known elevational distribution is from 975 to 1650 m.

**DESCRIPTION**—A medium-sized *Cryptotis*, HB averaging 69 (table 4); tail short, averaging 43% ( $\pm 1$ ,  $n = 23$ ) of HB; dorsal hairs usually about 4 mm long, ranging from 3 to 5 mm long, two-banded; dorsal and lateral pelage may be Olive Brown, Mummy Brown, or Clove Brown; venter is slightly paler than dorsum, Buffy Brown or Olive Brown.

Rostrum broad and moderately long (PL/CBL =  $43.4\% \pm 1.0$ ,  $n = 16$ ); interorbital area very broad; usually only one dorsal foramen (76%,  $n = 21$ ), normally located on the right frontal, medium to very large in size; a well-developed foramen typically present posterior to the dorsal articular facet on one (10%,  $n = 10$ ) or both (70%) sides of the skull; normally no foramen dorsal to dorsal articular facet (70%,  $n = 10$ ); anterior process of the petromastoid low and very narrow (fig. 18A); paroccipital process prominent; zygomatic plate broad in proportion to CBL (12.0%  $\pm 0.8$ ,  $n = 16$ ) and PL (27.5%  $\pm 2.1$ ,  $n = 23$ ); anterior border of zygomatic plate from posterior one-half of para-style/mesostyle valley to mesostyle of M1, posterior border from posterior one-half of mesostyle/metastyle valley of M2 to middle of M3, and from middle of base of maxillary process to posterior to maxillary process; palate wide; upper tooth row crowded; unicuspids massive; U4 normally displaced medially, so that U3 and P4 in contact or nearly so; U4 not visible in lateral view of skull; lateral view of U3 also sometimes partially obstructed by P4; posterior borders of P4, M1, and M2 unrecessed or only very slightly recessed; M3 with well-developed paracrista, and paracone, reduced precentrocrista, poorly developed and normally uncolored mesostyle and protocone, hypcone absent or vestigial and incorporated into the posterior cingulum; upper dentition quite bulbous.

Mandible large; horizontal ramus deep; coronoid process high (HCP/ML =  $76.8\% \pm 3.5$ ,  $n = 16$ ) and broad, joining mandible at a steep angle; horizontal and vertical branches of articular condyle short and broad; lower sigmoid notch very shallow; posterior border of lower incisor extends almost to posterior border of cingulum of p4; lower dentition wide and long; only hypoconid in talonid of m3.

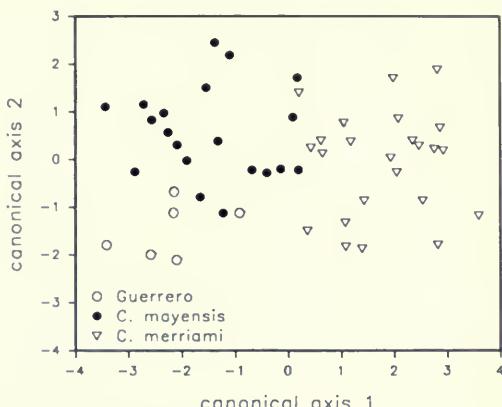


FIG. 9. Plot of specimens of *C. moyensis* from Guerrero and the Yucatan Peninsula and *C. merriami* on canonical axes 1 and 2 from discriminant function analysis of mandibular variables.

**COMPARISONS**—*Cryptotis mayensis*—*C. merriami* is approximately the same in overall size but has a darker pelage, which is dark brown in appearance rather than grayish brown; skull is much wider overall, especially the rostrum, interorbital area, braincase, and palate; upper dentition much broader; longer mandible; shorter coronoid process.

*Cryptotis magna*—*C. merriami* is much smaller (HB averaging 69 vs. 86; table 4) and a much shorter tail (averaging 43% of HB vs. 53%); skull much smaller in all dimensions but has a relatively broader zygomatic plate (averaging 12.0% of CBL vs. 10.1%  $\pm 0.6$ ); usually only one dorsal foramen; well-developed foramen posterior to dorsal articular facet; rarely possesses foramina dorsal to dorsal articular facet; coronoid process lower (averaging 76.8% of mandible length vs. 83.0%  $\pm 2.4$ ); no entoconid in talonid of m3.

*Cryptotis hondurensis*—*C. merriami* is much larger (HB averaging 69 vs.  $61 \pm 5$ ; table 4) and has a shorter, broader tail that is thick and rounder at the tip (rather than tapering to a point as in *C. hondurensis*); relatively shorter, broader rostrum; wider palate; M3 less complex, lacking metacone; dentition bulbous and upper and lower molars and unicuspids much more massive.

**REMARKS**—The dorsal pelage of *C. merriami* is indistinctly two-banded. The proximal five-sixths of the dorsal hairs is a medium steel gray; the distal tip is medium brown. In two specimens from Guatemala (UMMZ 117844, 117845), the pelage is darker overall than those from El Salvador. The tips of the hairs of the Guatemalan specimens are a darker brown.

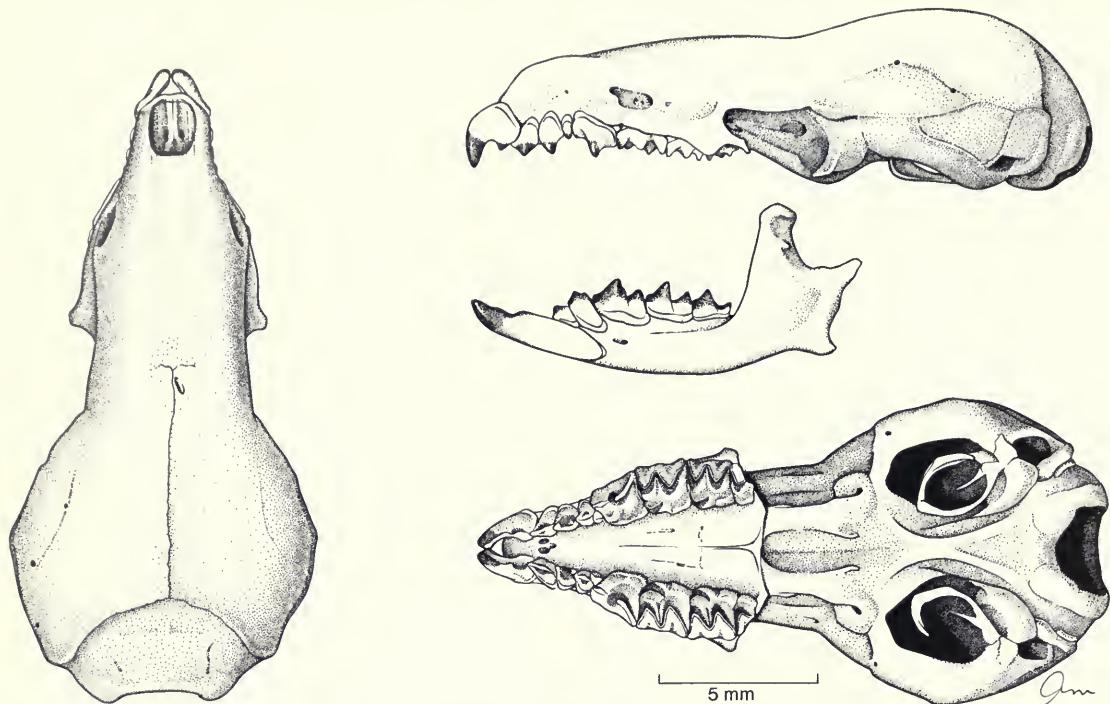


FIG. 10. Dorsal, ventral, and lateral views of the skull and mandible of *C. merriami* (MVZ 130335). Reprinted with permission of the Biological Society of Washington.

Two specimens of *C. merriami* merit discussion. A male (UMMZ 117111) from Santa María de Ostuma, Nicaragua, is the first specimen of the *C. nigrescens* complex to be identified from that country. This specimen was identified previously as *C. parva orophila* (Choate, 1970). A specimen of unknown sex from 4.5 km NE Tilarán (KU 84365) is the first record of this species from Costa Rica. It previously was referred to *C. n. nigrescens* (Choate, 1970). Both specimens display the large size, wide skull, broad zygomatic plate, robust mandible, and bulbous dentition characteristic of *C. merriami*. For this reason, we refer both to this species. They clearly are not referable to *C. nigrescens* or *C. parva orophila*. However, both specimens come from regions that are isolated geographically from the main range of *C. merriami* in Chiapas and northern Central America, and further study of larger series of specimens of this group may prove the shrews from Nicaragua and Costa Rica to be distinct. In addition, *C. merriami* and *C. nigrescens* may be sympatric or parapatric in parts of Costa Rica's Tilarán Cordillera.

To test the overall similarity of the two specimens of *C. merriami* from Santa María de Ostuma and Tilarán to *C. merriami* from the main part of its range and to Costa Rican *C. nigrescens*, we

carried out a PCA using seven cranial variables (ZP, IO, U1B, M2B, PL, TR, UTR) measured from the two specimens from Santa María de Ostuma and Tilarán, 21 *C. merriami*, and 20 randomly selected *C. nigrescens* from Monteverde. All variables weighed out heavily on factor 1, indicating that it is a good estimator of overall size. Factor 2 represented a contrast between UTR and negatively weighted IO (table 7). A plot of factor 1 vs. factor 2 scores from this analysis (fig. 12) shows the larger *C. merriami* clustering on the right half of the graph, and the smaller *C. nigrescens* are concentrated in the left half of the graph. The two species overlap completely on the shape axis (factor 2). The specimen of *C. merriami* from Santa María de Ostuma is intermediate in size, defining the lower size limit of *C. merriami*. The specimen from Tilarán plots well within the main scatter of *C. merriami*.

Specimens of *C. merriami* from Cerro Cacaguatique, El Salvador, are geographically isolated from the main range of the species. However, the lack of any morphological differentiation between specimens from Cerro Cacaguatique and other parts of the range argues against their being considered different taxa.

The habitat on Cerro Cacaguatique, as noted by

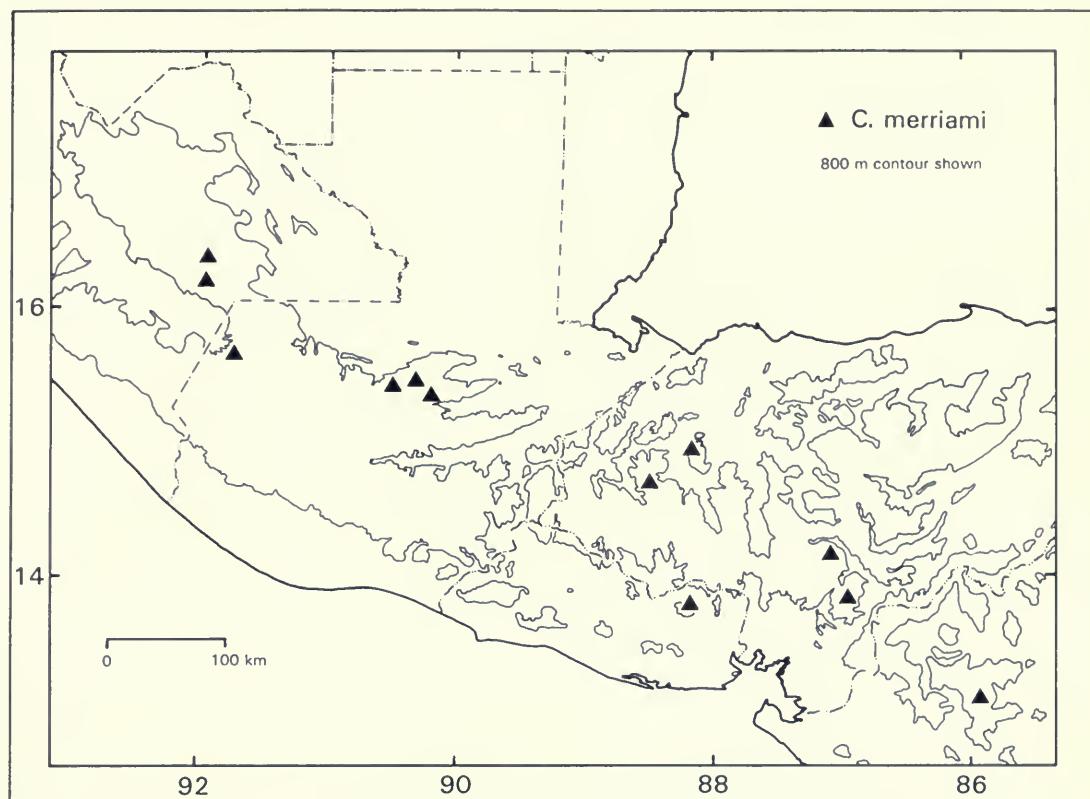


FIG. 11. Map of southern Mexico and northern Central America showing the distribution of *C. merriami*. See also Figure 14.

Burt and Stirton (1961), was oak forest with scattered pines from about 3500 ft [1065 m] up. Below that elevation, much of the area had been cleared for cultivation of coffee, bananas, and corn. Near the summit at 4000 ft [1220 m], epiphytes, ferns, and mosses occurred. Burt and Stirton (1961) reported taking *C. merriami* with *Heteromys desmarestianus*, *Ototylomys phyllotis*, and *Peromyscus mexicanus* along the rocky canyon slopes near the bottom, but specimen tags indicate that the shrews were taken from 3500 ft to the summit.

Goldman (1951) described the type locality of *C. merriami* as an indigenous village at an elevation of about 5400 ft [1645 m] and a little below the transition between the Humid Upper Tropical and Lower Austral or Upper Austral life zones. The locality is near the lower limit of cypress (*Cupressus*), but much of the region already had been deforested for cultivation of crops.

Few reproductive data are available for *C. merriami*, and no pregnant or lactating females have been recorded. Individual males collected on 23 May and 26 November had well-developed lateral

glands. Two males captured on 2 January and 17 December, respectively, had no evidence of glandular development.

#### *Cryptotis nigrescens* (J. A. Allen, 1895) (fig. 13)

*Blarina (Soriciscus) nigrescens* J. A. Allen, 8 November 1895, Bull. Amer. Mus. Nat. Hist. 7:339.

*Blarina micrura*; J. A. Allen, 22 September 1893, Bull. Amer. Mus. Nat. Hist. 5:238.

TABLE 7. Factor loadings from PCA of cranial variables of *C. merriami* and *C. nigrescens*.

Variable	Factor 1	Factor 2
PL	0.932	-0.112
TR	0.920	0.053
M2B	0.920	-0.231
U1B	0.909	-0.076
IO	0.869	-0.288
UTR	0.793	0.549
ZP	0.776	0.196

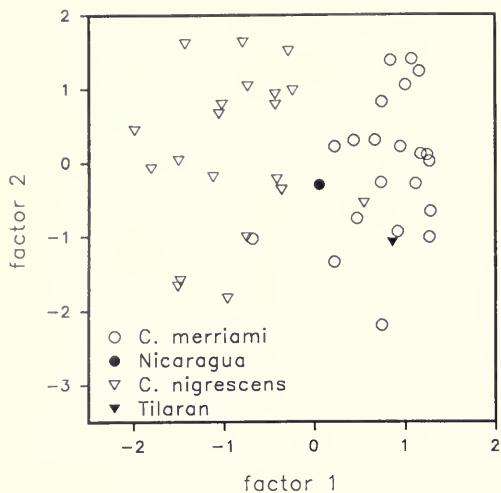


FIG. 12. Plots of principal components factor scores of *C. merriami* and *C. nigrescens* on factor axes 1 and 2.

*Blarina nigrescens*: C. H. Merriam, 31 December 1895, N. Amer. Fauna 10:31.

*Cryptotis nigrescens*: G. S. Miller, Jr., 31 October 1911, Proc. Biol. Soc. Washington 24:222.

*Cryptotis nigrescens*: G. G. Goodwin, 10 December 1944, Amer. Mus. Novitates 1267:1; G. G. Goodwin, 31 December 1946, Bull. Amer. Mus. Nat. Hist. 87:288; H. W. Setzer, 29 September 1950, J. Washington Acad. Sci. 40:300; E. R. Hall and K. R. Kelson, 31 March 1959, The Mammals of North America 1:63 (part); C. O. Handley, Jr., 22 November 1966, Checklist of the mammals of Panama, in R. L. Wenzel and V. J. Tipton (eds.), Ectoparasites of Panama, p. 756.

*Cryptotis zeteki*: H. W. Setzer, 29 September 1950, J. Washington Acad. Sci. 40:299; G. G. Goodwin, 28 June 1954, Amer. Mus. Novitates 1677:2; E. R. Hall and K. R. Kelson, 31 March 1959, The Mammals of North America 1:62.

*Cryptotis tersus*: G. G. Goodwin, 28 June 1954, Amer. Mus. Novitates 1677:1; E. R. Hall and K. R. Kelson, 31 March 1959, The Mammals of North America 1:64.

*Cryptotis nigrescens zeteki*: C. O. Handley, Jr., 22 November 1966, Checklist of the mammals of Panama, in R. L. Wenzel and V. J. Tipton (eds.), Ectoparasites of Panama, p. 756.

*Cryptotis parva orophila*: J. R. Choate, 30 December 1970, Univ. Kansas Publ. Mus. Nat. Hist. 19:262 (part).

*Cryptotis nigrescens nigrescens*: J. R. Choate, 30 December 1970, Univ. Kansas Publ. Mus. Nat. Hist. 19:279 (part); E. R. Hall, 3 April 1981, The Mammals of North America 1:63 (part).

**HOLOTYPE**—Skin and skull of subadult, sex unknown, American Museum of Natural History no. 9591/7952, collected by G. K. Cherrie (collector number 2004) 5 September 1891 from Costa Rica, San José Province, San Isidro.

**DISTRIBUTION**—Occurs in highlands above 800 m in Costa Rica and western Panama (fig. 14). In Costa Rica, *C. nigrescens* is known from the Tilarán, Central, and Talamanca cordilleras; in Panama, it is known from the Chiriquí Cordillera. The known elevational distribution in Costa Rica is from 870 to 2865 m; in Panama, it is 820 to 2150 m.

**DESCRIPTION**—A small to medium *Cryptotis*, HB averaging 68 (table 4); tail short, averaging 43% ( $\pm 5$ , n = 70) of HB; snout in fluid-preserved specimens short and broad; dorsal hairs approximately 4.5 mm long, ranging from 4 to 5 mm, two-banded; pelage coloration varies somewhat geographically; dorsal and lateral pelage Mummy Brown or Clove Brown; ventral pelage slightly paler, Buffy Brown, Saccardo's Umber, Olive Brown, or Mouse Gray.

Rostrum narrow and of normal length (PL/CBL =  $42.6\% \pm 0.8$ , n = 70); interorbital area of moderate breadth; often two dorsal foramina (68%, n = 59), small to large size, positioned close to suture between frontals; normally no foramen posterior to the dorsal articular facet (88%, n = 57); usually a well-developed foramen dorsal to external capitular facet on one (2%, n = 57) or both (93%) sides of the skull, but foramen may be minute (3%); anterior process of the petromastoid very low and very narrow (fig. 18B); paroccipital process prominent; zygomatic plate narrow in proportion to CBL ( $10.5\% \pm 0.9$ , n = 75) and PL ( $24.8\% \pm 2.1$ ); anterior border of zygomatic plate from mesostyle to mesostyle/metastyle valley of M1, posterior border at posterior one-half of mesostyle/metastyle of M2 to middle of M3, and usually at middle of base of maxillary process, but can occur from anterior one-half of this process to posterior to the process; palate moderately wide; upper tooth row not especially crowded; U4 normally in line of unicuspis tooth row, preventing contact between U3 and P4; U4 usually obscured by P4 in lateral view, but often partly visible; posterior borders of P4, M1, and M2 unrecessed or only slightly recessed; M3 with well-developed paracrista, and paracone, reduced precentrocrista and mesostyle, poorly developed, but often colored postcentrocrista and metacone (but postcentrocrista short with mesostyle and metacone closely associated), protocone present and often colored, poorly developed hypocone often present; dentition not bulbous.

Mandible of moderate length and breadth; coronoid process low (HCP/ML =  $71.7\% \pm 2.6$ , n = 70) and narrow, joins mandible at a steep angle;

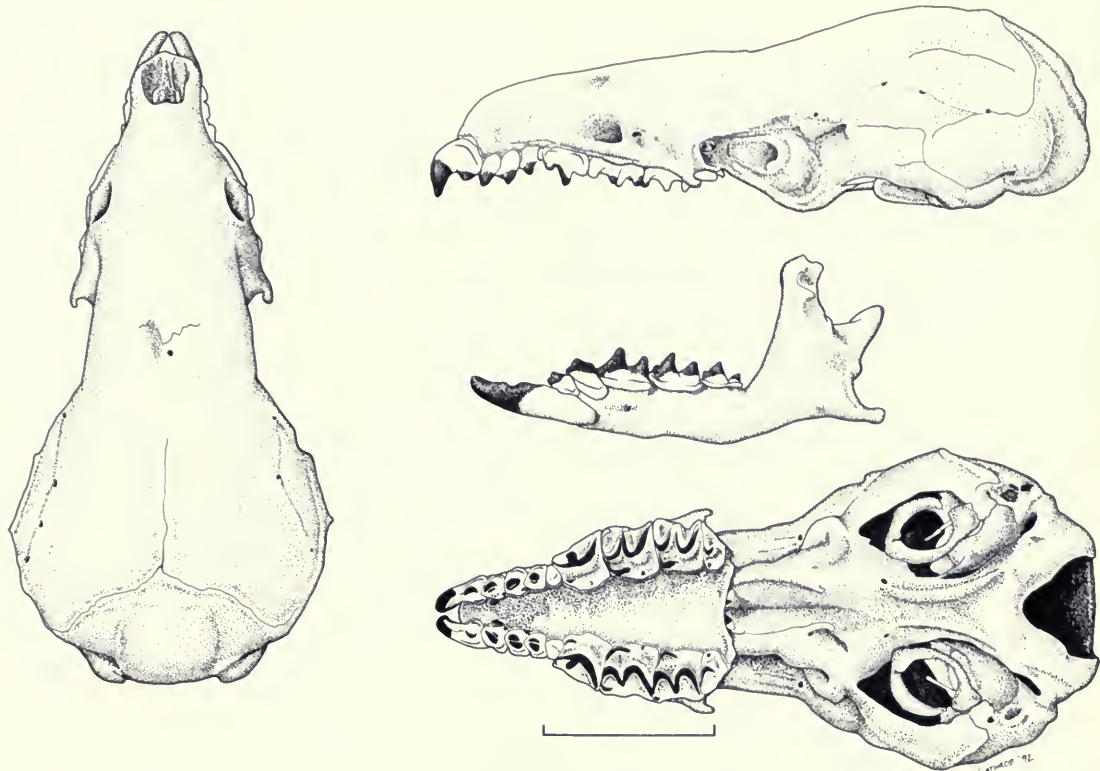


FIG. 13. Dorsal, ventral, and lateral views of the skull and mandible of *C. nigrescens* (KU 143389). Scale bar = 5 mm.

articular condyle relatively short and narrow; lower sigmoid notch very shallow; posterior border of lower incisor almost to posterior border of cingulum of p4; vestigial entoconid occasionally present (38%, n = 50) in talonid of m3.

**COMPARISONS**—*Cryptotis nigrescens* is the only member of the *C. nigrescens* complex sometimes possessing an entoconid in the talonid of m3.

***Cryptotis mayensis***—*C. nigrescens* has a much darker pelage, dark brown in appearance rather than grayish brown; skull is less robust; rostrum not as broad; anterior process of the petromastoid lower; foramen associated with ventral branch of sinus canal normally absent; foramen dorsal to dorsal articular facet of skull normally present; much more likely to have two dorsal foramina, one on each frontal; relatively and absolutely narrower zygomatic plate, anterior border of which is positioned more posteriorly relative to upper tooth row; palate relatively wider; upper dentition not as massive, unicuspids not as broad; upper molars relatively longer; unicuspид tooth row less crowded; mandible relatively longer and more slender; coronoid process shorter and narrower;

branches of articular process narrower; lower molars relatively longer; hypoconid sometimes present on m3.

***Cryptotis magna***—*C. nigrescens* is much smaller (HB averaging 68 vs. 86; table 4) and has a much shorter tail (averaging 43% of HB vs. 53%); skull much smaller in all dimensions; foramen associated with ventral branch of sinus canal normally absent; coronoid process much lower (averaging 71.7% of ML vs. 83.0%  $\pm$  2.4); dentition not bulbous.

***Cryptotis merriami***—*C. nigrescens* has a generally darker pelage; skull is not nearly as robust, much narrower overall, especially the rostrum, interorbital area, braincase, and palate; foramen associated with ventral branch of sinus canal normally absent; anterior process of the petromastoid lower; relatively and absolutely narrower zygomatic plate; upper dentition absolutely smaller, narrower, less massive; unicuspids not as broad; upper molars relatively longer; unicuspids tooth row less crowded; M3 slightly more developed, possessing minute postcentrocrista and metacone; mandible shorter and more slender; coronoid process shorter and narrower; branches of articular

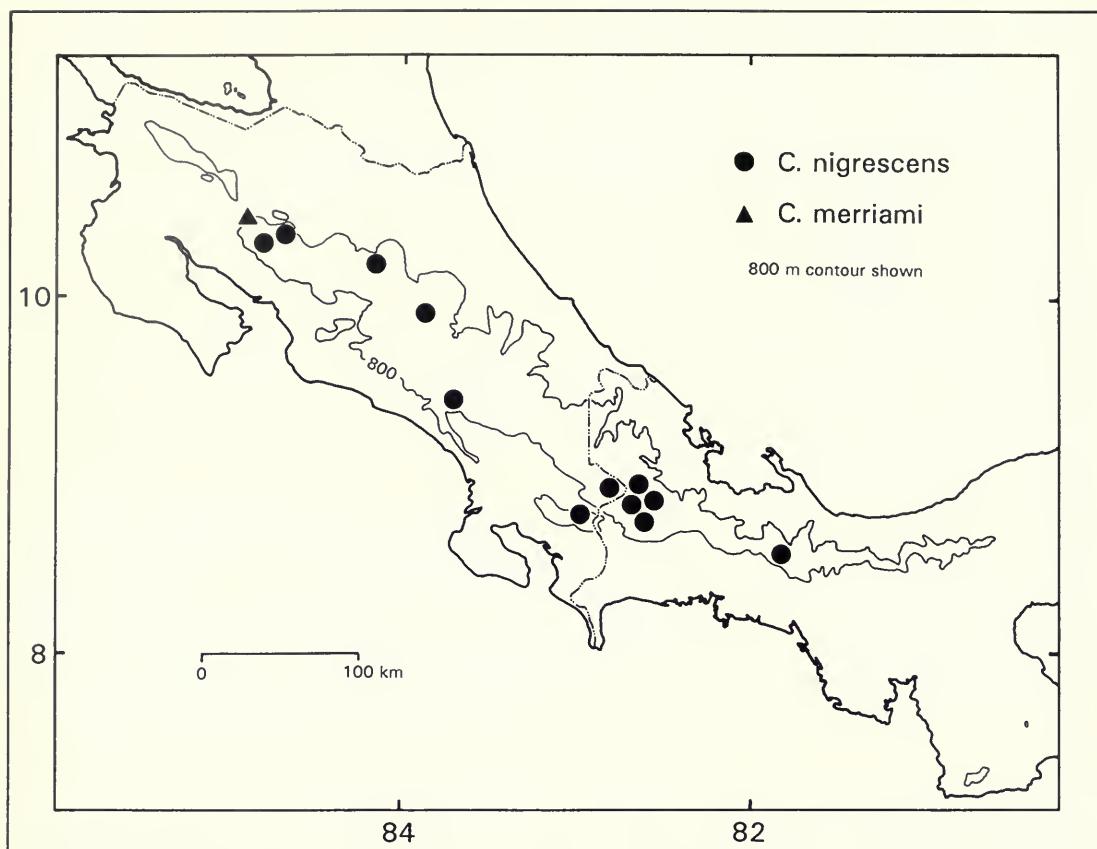


FIG. 14. Map of Costa Rica and western Panama showing the distribution of *C. nigrescens*.

process narrower; lower molars narrower; hypoconid sometimes present on m3.

***Cryptotis hondurensis***—*C. nigrescens* is larger (HB averaging 68 vs.  $61 \pm 5$ ; table 4); shorter tail (averaging 41% of HB vs. 46%); foramen associated with ventral branch of sinus canal normally absent; M3 less complex, lacking metacone; coronoid process of mandible lower; vestigial entoconid sometimes present on m3.

**REMARKS**—Viewed anteriorly, the pelage of *C. nigrescens* is very reflective. The resulting sheen distorts the hues, making colors appear paler, especially on the venter. Dorsal pelage of *C. nigrescens* appears two-banded. The proximal three-quarters of the hairs is medium steel gray; the remaining distal portion is dark brown. In general, specimens from Costa Rica have slightly darker pelage, from Mummy Brown to Bone Brown and Clove Brown dorsally with a Buffy Brown or Olive Brown venter. Specimens from western Panama are Mummy Brown dorsally with a venter of Buffy

Brown, Saccardo's Umber, or Sepia in the Chiriquí highlands. The darkest specimens are two shrews (USNM 520692, 520693) from Fish Camp, Bocas del Toro Province, Panama, which are Blackish Brown 2 dorsally and Deep Grayish Olive ventrally. They are in contrast to the slightly paler specimens from other localities in western Panama. These two specimens from Fish Camp also have very long tails (52–53% of HB). However, both are young animals with nearly unworn dentition, and this may account for the differences between them and other *C. nigrescens* from Panama.

There is a fair amount of variation between the large series of *C. nigrescens* from Monteverde, Costa Rica, and those from near San Félix (including Cerro Bollo), Panama. Specimens from Monteverde and from San Félix differ greatly in size (table 1). In addition, the presence of a hypoconid on m3 is much more prevalent in the Panamanian series (71%, n = 14) than in the Mon-

teverde specimens (25%, n = 32), and two dorsal foramina are present more often in specimens from near San Félix (94%, n = 16) than in those from Costa Rica (58%, n = 43). Further collecting and study of Panamanian and Costa Rican *Cryptotis* may show that *C. nigrescens* is a complex of species.

Specimens of *C. nigrescens* from Cinchona and Monteverde, Costa Rica, and from Santa Clara and Boquete Trail on Cerro Punta, Panama, previously were identified as *C. parva orophila* (Choate, 1970). The small size of Costa Rican *C. nigrescens* and the simple M3 can make the two species difficult to separate. *Cryptotis nigrescens* can be distinguished by its much darker pelage coloration, on both venter and dorsum, and by its relatively longer tail ( $43\% \pm 5$  of HB in *C. nigrescens* vs.  $33\% \pm 4$ , n = 11). In addition, *C. nigrescens* has a longer zygomatic plate, the posterior margins of P4, M1, and M2 are not as deeply recessed, M3 possesses a reduced metacone, and there is sometimes a hypoconid on m3. Our correction of these identifications means that *C. parva* presently is not known south of Costa Rica.

Setzer (1950) gave the location of Cerro Punta, the type locality of *C. zeteki* (a junior synonym of *C. nigrescens*) as  $8^{\circ}42'N$ ,  $82^{\circ}48'W$ . Based on recent maps and gazetteers, the community is located at  $8^{\circ}34'N$ ,  $81^{\circ}50'W$ .

Hall's (1981, p. 63) map of the distribution of *C. nigrescens* implies that the species is found throughout Costa Rica, including low elevations along both coasts (with the exception of the Nicoya and Osa peninsulas), and throughout much of central and eastern Panama. *Cryptotis nigrescens*, as we understand it today, inhabits only higher elevations, and it is restricted to the Tilarán, Central, and Talamanca cordilleras of Costa Rica and the Chiriquí Cordillera of Panama. At Monteverde the species occurs in cloud forest, in forest fragments, and in pastures from 870 to 1660 m, and in western Panama it has been taken in cloud forest, disturbed cloud forest, elfin woodland, and drier Pacific slope forest from 1275 to 1856 m. The known upper elevational range for *C. nigrescens* is 2865 m. This probably approaches the true upper range for the species, because collections of shrews from higher elevations do not include this species. *Cryptotis gracilis* is known from 2435 to 3536 m in the Talamanca and Chiriquí highlands, and *C. jacksoni*, a member of the *C. gracilis* complex, has been taken from 2350 to 3180 m on Volcán Irazú (Woodman, 1992). That this is not a simple case of competitive exclusion is suggested by the fact that *C. nigrescens* and *C. gracilis* over-

lap in their elevational range and that both have been collected from the same locality in Panama (R. Pine, pers. comm.).

In the Monteverde area, we found *C. nigrescens* in a variety of habitat types including Tropical Premontane Rain Forest, Tropical Premontane Moist Forest, Tropical Premontane Wet Forest, and Tropical Lower Montane Wet Forest. Common small mammals in these habitats include *Peromyscus nudipes*, *Heteromys desmarestianus*, *Scotinomys teguina*, and *Reithrodontomys creper* and *Oryzomys albibarbis* at the higher elevations. A second, undescribed species of small-eared shrew occurs at the higher elevations in the Monteverde Cloud Forest. This is a much larger shrew and is a member of the *C. gracilis* complex. At this point, we cannot say whether these two species are truly syntopic, although they are sympatric in this area. *Cryptotis nigrescens* probably is abundant at Monteverde but is infrequently observed and difficult to capture. During several weeks of fieldwork in 1989, we had over 1,570 trapnights using a combination of Sherman live traps, Museum Specials, and common snap traps baited with a mixture of suet, seeds, raisins, and vanilla, and over 500 trapnights using pitfalls with drift fences. Of a total of 24 shrews we obtained, none were captured in baited traps, 8 were taken in our pitfalls, 5 more were captured in pitfalls set by entomologists in a study apart from ours, 3 were brought in by domestic cats, and 8 were encountered dead on a trail or road by local residents prior to our arrival.

Few reproductive data are available for *C. nigrescens*. A female (USNM 516623) from east of Cerro Pando was recorded as "recently lactating" on 16 March 1973, and a lactating female (USNM 516620) was collected at Santa Clara, western Panama, on 25 March 1972. We captured an adult female (KU 143389) with three embryos (crown-rump length = 4 mm) at Monteverde on 12 May 1989 and another with an enlarged uterus on 21 May (KU 143396), suggesting that it had recently given birth. Two females (USNM 541044, 541030), pregnant with a single embryo each (crown-rump length = 15 mm, 5 mm), were taken on 2 and 4 July 1980, respectively, 24–24.5 km NNE of San Félix, western Panama. Females without embryos have been captured between 9 and 23 May at Monteverde (n = 6) and on 13 and 26 June in Panama (n = 2). Our inspection of male *C. nigrescens* shows well-developed lateral glands on 20 individuals collected from 9 May through 1 July. Individual males without well-developed lateral glands were collected on 26 February, 7 March, 11 March, 3

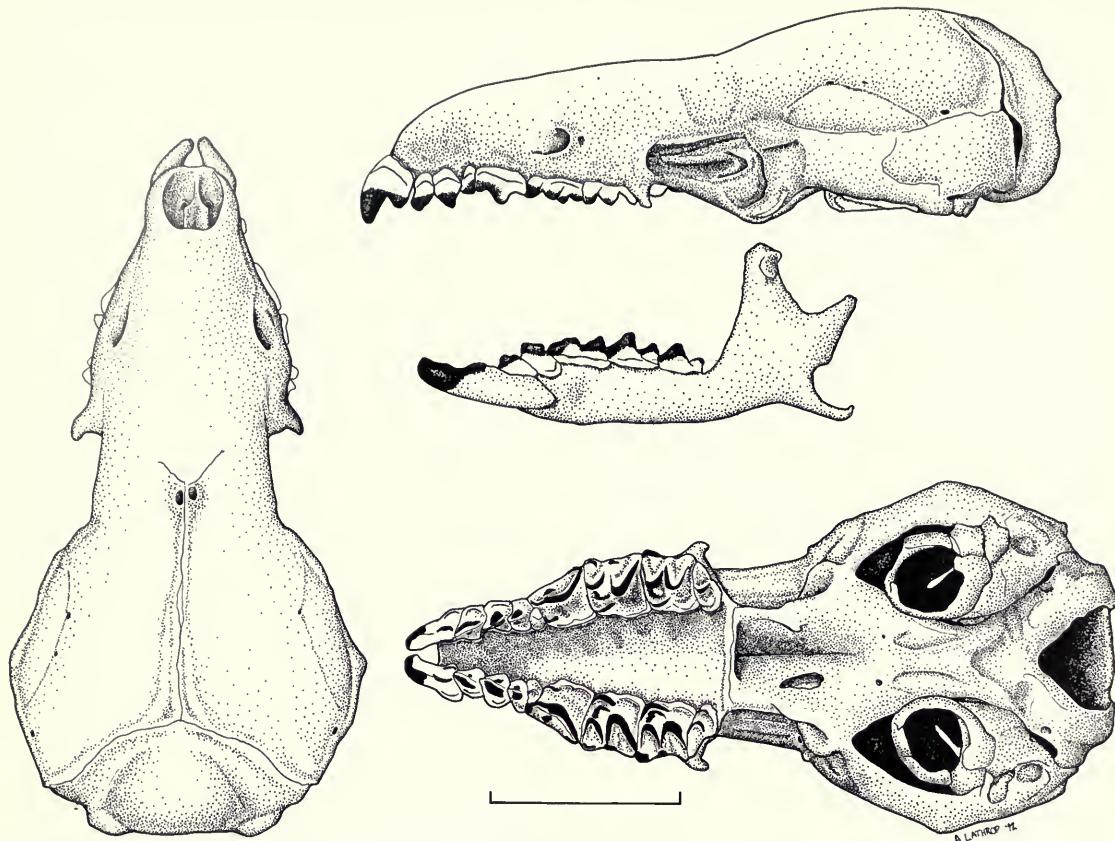


FIG. 15. Dorsal, ventral, and lateral views of the skull and mandible of *C. mera* (USNM 337969). Scale bar = 5 mm.

April, 28 July, and 4 July. On 9 and 18 May we recorded individual males from Monteverde with melanistic sheaths surrounding the testes; both animals had well-developed lateral glands and enlarged testes ( $3.5 \times 2.5$  mm and  $4 \times 2.5$  mm, respectively).

A young adult female (KU 143393) captured at Monteverde on 15 May 1989 lacks digits on its right forefoot. The vestigial first digit is the only one bearing a claw, and this is poorly formed. The shape of the foot suggests that the digits were never fully developed during ontogeny rather than lost later due to an accident.

#### *Cryptotis mera* Goldman, 1912 (fig. 15)

*Cryptotis merus* E. A. Goldman, 20 September 1912, Smiths. Misc. Coll. 60(2):17; E. A. Goldman, 24 April 1920, Smiths. Misc. Coll. 69(5):171; H. W. Setzer, 29 September 1950, J. Washington Acad. Sci. 40:300; G. G. Goodwin, 28 June 1954, Amer. Mus. Novitates 1677:2.

*Cryptotis mera*: E. R. Hall and K. R. Kelson, 31 March 1959, The Mammals of North America 1:61.

*Cryptotis nigrescens mera*: C. O. Handley, Jr., 22 November 1966, Checklist of the mammals of Panama, in R. L. Wenzel and V. J. Tipton (eds.), Ecoparasites of Panama, p. 756.

*Cryptotis nigrescens nigrescens*: J. R. Choate, 30 December 1970, Univ. Kansas Publ. Mus. Nat. Hist. 19:279 (part); E. R. Hall, 3 April 1981, The Mammals of North America 1:63 (part).

**HOLOTYPE**—Skin and skull of an adult male, U.S. National Museum of Natural History no. 178976, collected by E. A. Goldman (original number 21669) 2 May 1912 from Panama, Darién Province, Mount Pirri [Cerro Pirre], near head of Río Limón, 4500 ft.

**DISTRIBUTION**—Cerro Tacarcuna and Cerro Malí in the eastern Serranía de Darién, and Cerro Pirre in the Serranía de Pirre (fig. 17). The species undoubtedly occurs in Colombia, but all specimens currently known are from the Panamanian side of the border. The recorded elevational distribution of the species is 1370–1525 m.

**DESCRIPTION**—A medium-sized *Cryptotis*, HB averaging 69 (table 4); tail short, averaging 39% ( $\pm 2$ ,  $n = 6$ ) of HB; dorsal hairs approximately 4 mm long, ranging from 3.5 to 4.5 mm, indistinctly two-banded; dorsal and lateral pelage Mummy Brown; ventral pelage slightly paler, Saccardo's Umber or Mouse Gray.

Rostrum of normal length ( $PL/CBL = 42.4\% \pm 1.1$ ,  $n = 5$ ); interorbital area of moderate breadth; often two dorsal foramina (66%,  $n = 6$ ), not normally equal in size, positioned close to suture between frontals; normally no foramen posterior to the dorsal articular facet (100%,  $n = 4$ ); usually a well-developed foramen dorsal to dorsal articular facet on both sides of the skull (75%,  $n = 4$ ), but foramen may be minute (25%); anterior process of petromastoid very low and very narrow (fig. 18B); paroccipital process prominent; zygomatic plate narrow in proportion to CBL ( $11.0\% \pm 0.7$ ,  $n = 5$ ) and PL ( $26.0\% \pm 1.3$ ,  $n = 6$ ); anterior border of zygomatic plate at mesostyle/metastyle valley of M1, posterior border at metastyle of M2 to middle of M3, and from anterior edge to posterior edge of maxillary process; palate moderately wide; upper tooth row crowded; unicuspids massive; U4 normally displaced medially, so U3 and P4 in contact or nearly so; U4 usually not visible in lateral view; lateral view of U3 also often partly obstructed by P4; posterior borders of P4, M1, and M2 only slightly recessed; M3 with well-developed paracrista and paracone, reduced precentrocrista, mesostyle and postcentrocrista poorly developed and normally uncolored, protocone present and often colored, hypocone poorly developed, appearing as a posterior cingulum; dentition quite bulbous.

Mandible of moderate length and breadth; coronoid process high ( $HCP/ML = 76.3\% \pm 4.8$ ,  $n = 6$ ), but narrow, joins mandible at fairly steep angle; articular condyle relatively short and broad; lower sigmoid notch very shallow; posterior border of lower incisor almost to posterior border of cingulum of p4; only hypoconid in talonid of m3.

**COMPARISONS**—*Cryptotis mayensis*—*C. mera* has a much darker pelage, dark brown in appearance rather than grayish brown; skull is much shorter, but interorbital area much broader; foramen associated with ventral branch of sinus canal absent; palate relatively wider; anterior process of the petromastoid lower; foramen associated with ventral branch of sinus canal normally absent; foramen dorsal to dorsal articular facet of skull normally present; much more likely to have two dorsal foramina, one on each frontal; mandible more

slender; coronoid process shorter and much narrower; lower molars relatively longer.

*Cryptotis magna*—*C. mera* is much smaller (HB averaging 69 vs. 86; table 4) and has a much shorter tail (averaging 39% of HB vs. 53%); skull much smaller in all dimensions; coronoid process lower (averaging 76.3% of mandible length vs.  $83.0 \pm 2.4$ ); no entoconid in talonid of m3.

*Cryptotis merriami*—*C. mera* is much smaller in nearly all cranial dimensions; foramen associated with ventral branch of sinus canal absent; relatively broader palate; anterior process of the petromastoid lower; mandible not as deep; coronoid process much narrower.

*Cryptotis hondurensis*—*C. mera* is larger (HB averaging 69 vs.  $61 \pm 5$ ; table 4) and has a shorter tail (averaging 39% of HB vs. 46%); foramen associated with ventral branch of sinus canal absent; M3 less complex, lacking metacone; dentition bulbous.

*Cryptotis nigrescens*—*C. mera* has a relatively wider skull, especially in the interorbital area, and palate; relatively longer zygomatic plate; more crowded upper tooth row; relatively shorter, deeper mandible; no hypoconid on m3.

**REMARKS**—Choate (1970) considered *C. mera* a junior synonym of *C. nigrescens nigrescens*. At the time of his study, however, he had a total of only 29 specimens at hand. Recent collection of large series of *C. nigrescens* from Costa Rica and western Panama permitted us to make more extensive comparisons, and we recognize *C. mera* as a distinct species.

Dorsal pelage of *C. mera* is two-banded and is generally similar to that of *C. nigrescens* from western Panama in color.

*Cryptotis mera* is known from cloud forest on two mountain areas isolated from each other by lowlands below 200 m. Specimens from the Serranía de Pirre have a shorter coronoid process ( $HCP/ML = 71\%$ ,  $n = 2$ ) than those from the Serranía de Darién ( $79\% \pm 3$ ,  $n = 4$ ), but are otherwise indistinguishable. Populations from these two areas may prove to be distinct once additional specimens are available, but at this time we consider them to be conspecific.

The holotype and two topotypes of *C. mera* were collected between 4500 and 5000 ft [1370 and 1525 m] in the Serranía de Pirre. Goldman (1912) described the region as covered with unbroken forest and having a seasonal but very heavy annual rainfall. Although little actual rain falls during the dry season, clouds normally envelop the upper elevations, providing moisture year-round.

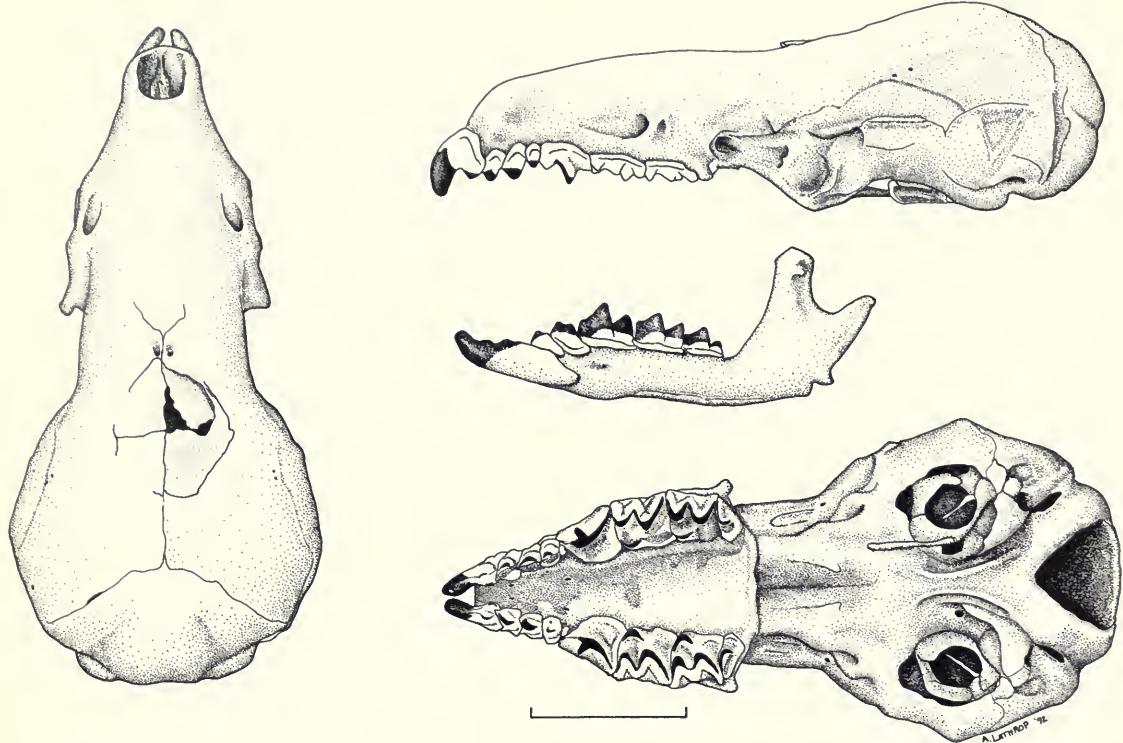


FIG. 16. Dorsal, ventral, and lateral views of the skull and lateral view of the skull and mandible of *C. colombiana* (FMNH 69816). Scale bar = 5 mm.

Reproductive data for *C. mera* are scarce. Two females (USNM 337966, 337969) from Cerro Malí and Cerro Tacarcuna were lactating on 12 February and 11 March 1964, respectively.

Although Goldman (1912) originally published this species name as "merus," the correct spelling is "mera." *Cryptotis* is feminine, dictating that the feminine ending be used on all adjectival species names used in combination with it (Woodman, 1993).

#### *Cryptotis colombiana*, new species (fig. 16)

**HOLOTYPE**—Skin and skull of adult female, Field Museum of Natural History no. 69816, collected 15 October 1950 by Philip Hershkovitz (original no. 4723). Skull nearly complete, but with a puncture hole in the dorsal braincase; skin in very good condition, but missing a small patch of fur on left venter, some fur matted.

**TYPE LOCALITY**—Colombia; Central Cordillera; Antioquia Dept., Sonsón; 15 km E of Río Negrito; 1750 m.

**DISTRIBUTION**—At present, known only from type locality (fig. 17).

**DIAGNOSIS**—A small to medium-sized *Cryptotis* with very dark fur, a short tail, broad rostrum, palate, and interorbital area, foramen dorsal to dorsal articular facet but not posterior to this facet, petromastoid with broad anterior process and with large foramen in tympanic process, narrow zygomatic plate, crowded tooth row, bulbous and unrecessed dentition, simple M3, long mandible with a broad coronoid process that joins the horizontal ramus at nearly a right angle, short and broad articular condyle with no notch between the articular facets, shallow lower sigmoid notch, and lacking entoconid in talonid of m3.

**DESCRIPTION OF HOLOTYPE**—A small to medium-sized *Cryptotis*, HB = 76 (table 4); tail short, 36% of HB; dorsal hairs approximately 4–5 mm long, two-banded; dorsal and lateral pelage Olive Brown to Fuscous; ventral pelage only slightly paler, Buffy Brown to Hair Brown.

Rostrum broad and of normal length (PL/CBL = 44%); interorbital area broad; two large dorsal foramina, close to sagittal suture; no foramen pos-

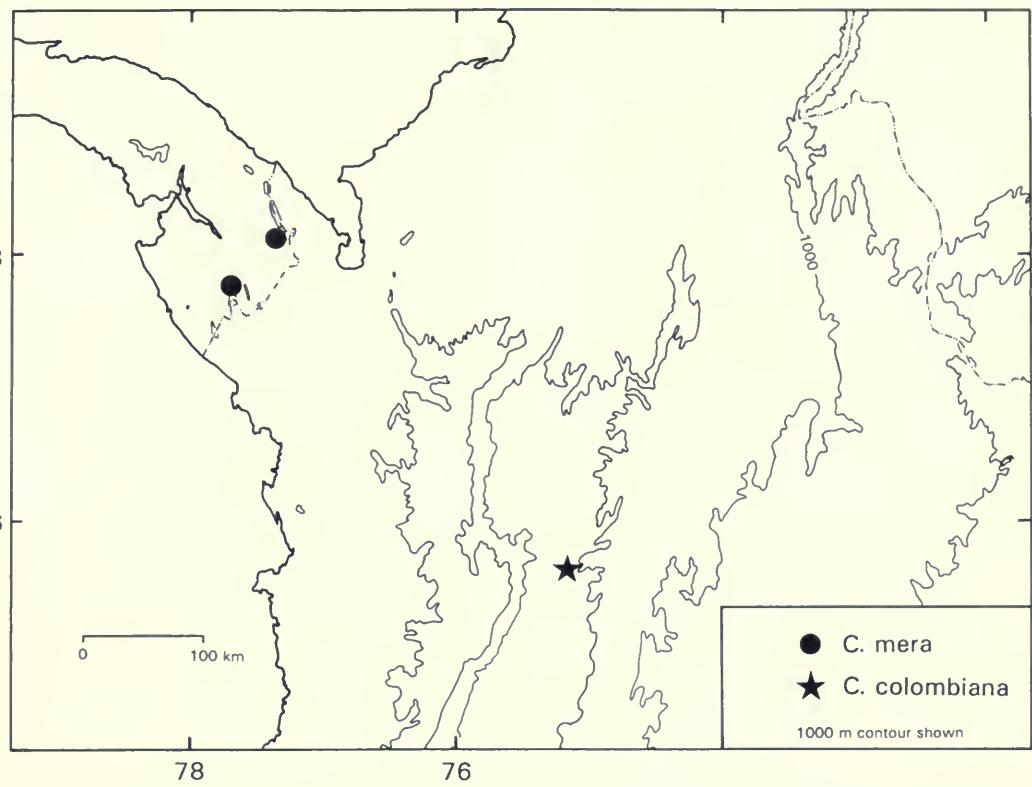


FIG. 17. Map showing the distribution of *C. mera* along the Panama/Colombia border and the type locality of *C. colombiana* in the Central Cordillera of Colombia.

terior to the dorsal articular facet; a moderately well-developed foramen dorsal to dorsal articular facet on both sides of the skull; anterior process of the petromastoid high and wide (fig. 18C); large foramen on posterior edge of tympanic process of petromastoid; paroccipital process low; zygomatic plate narrow in proportion to CBL (10.1%) and PL (22.7%); anterior border of zygomatic plate at posterior of mesostyle/metastyle valley of M1, posterior border at parastyle of M3 and anterior to posterior edge of base of maxillary process; palate wide; upper tooth row crowded; U4 reduced and peglike; U4 in line with other unicuspids, but too small to prevent contact between U3 and P4; U4 and corner of U3 obscured by P4 in lateral view; posterior borders of P4, M1, and M2 only slightly recessed; M3 with well-developed parastrista and paracone, reduced precentrostrista that joins the posterior cingulum; protocone of M3 poorly developed and uncolored; hypocone of M3 absent or part of posterior cingulum; dentition bulbous.

Mandible relatively long and of moderate breadth; coronoid process broad and low ( $HCP/ML = 69.6\%$ ) joining mandible at nearly a right angle; articular condyle distinctive: short and broad, lacking a lingual notch between the dorsal and ventral articular surfaces; lower sigmoid notch very shallow; posterior border of lower incisor almost to posterior border of posterior cingulum of p4; only hypoconid in talonid of m3.

**COMPARISONS**—*Cryptotis colombiana* is larger than any of the four species previously referred to *C. nigrescens*, and it differs from those species, *C. hondurensis*, and *C. magna* in having a shorter tail, a much broader and higher anterior process of the petromastoid (fig. 18); a large foramen on posterior edge of tympanic process of petromastoid; a lower, less prominent paroccipital process; and no distinct notch between the articular facets of the articular condyle of the mandible.

***Cryptotis mayensis***—*C. colombiana* has a much darker pelage, dark brown in appearance rather than grayish brown; a moderately well-developed

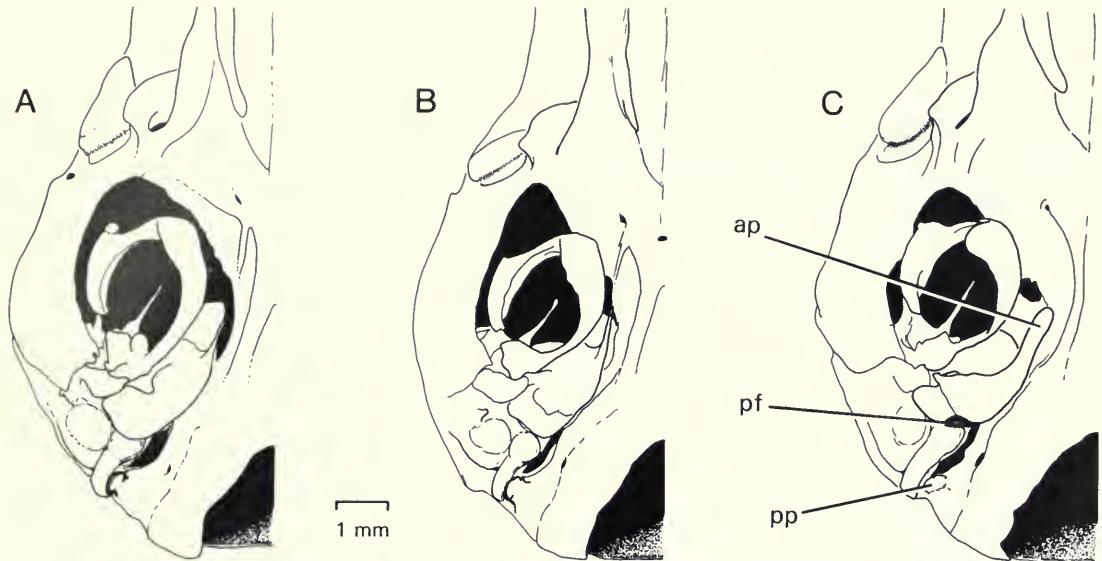


FIG. 18. Ventral view of the right tympanic region of the skulls of *C. merriami* (A, UMMZ 117845), *C. nigrescens* (B, KU 143385), and *C. colombiana* (C, FMNH 69816), illustrating the location and relative development of the anterior process of the petromastoid (ap) and the paroccipital process (pp), and the foramen on the posterior edge of the tympanic process of the petromastoid (pf).

foramen dorsal to the dorsal articular facet, but no foramen posterior to this facet; relatively narrower zygomatic plate; shorter unicuspids tooth row and longer molariform tooth row; broader interorbital area and much broader palate; smaller unicuspids; much shorter and much narrower coronoid process; longer mandible.

**Cryptotis magna**—*C. colombiana* is much smaller (HB = 76 vs. 86; table 4) and has a much

shorter tail (36% of HB vs. 53%); skull much smaller in all dimensions; coronoid process much lower (averaging 69.6% of ML vs.  $83.0\% \pm 2.4$ ); no entoconid in talonid of m3.

**Cryptotis merriami**—*C. colombiana* has a moderately well-developed foramen dorsal to the dorsal articular facet, but no foramen posterior to this facet; wider palate; relatively narrower zygomatic plate; longer molariform tooth row; much shorter and narrower coronoid process; longer mandible.

**Cryptotis hondurensis**—*C. colombiana* is much larger (HB = 76 vs.  $61 \pm 5$ ; table 4) and has a relatively shorter tail (36% of HB vs. 46%); foramen associated with ventral branch of sinus canal normally absent; narrower zygomatic plate (10.1 vs. 11.5); M3 less complex, lacking metacone; coronoid process of mandible lower; dentition bulbous.

**Cryptotis nigrescens**—*C. colombiana* differs in its much broader interorbital area and palate; longer molariform tooth row; somewhat broader coronoid process; dentition bulbous.

**Cryptotis mera**—*C. colombiana* has a broader interorbital area and somewhat broader palate; relatively narrower zygomatic plate; much longer molariform tooth row; shorter, broader coronoid process; longer mandible.

**REMARKS**—*Cryptotis colombiana* is the only species of the *C. nigrescens* group that is known to occur in South America, although *C. mera* un-

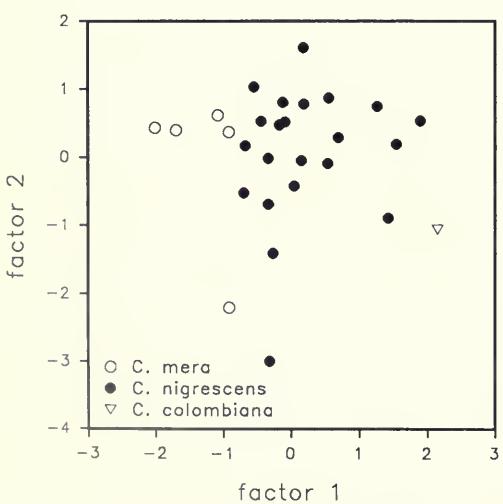


FIG. 19. Plot of principal components factor scores of *C. colombiana*, *C. mera*, and *C. nigrescens* on factor axes 1 and 2.

doubtedly occurs in Colombia along the Panamanian border. Based on the structure of the mandible and characteristics of the skull and teeth, both species clearly are more closely related to the *C. nigrescens* group than to any of the South American species. *Cryptotis colombiana* and *C. mera* are considerably smaller than any other described South American *Cryptotis*, and they are also the only two South American shrews with a short, broad articular condyle, and a nearly right angle junction between the coronoid process and the body of the mandible. All other described species of *Cryptotis* from South America have a high, narrow articular process and a mandible with a wide internal angle between the coronoid process and the horizontal ramus. In addition, *Cryptotis colombiana* is distinctive in being the only species known to lack a notch between the two articular facets of the articular condyle and a high, very broad anterior process of the petromastoid. The occurrence of *C. colombiana* on the Central Cordillera of Colombia suggests that it, or another closely related species, is likely to occur at high elevations in the Western Cordillera, which is located between the known geographic ranges of *C. colombiana* and *C. mera*.

To test the overall similarity of *C. colombiana* to that of the other, geographically closest members of the *C. nigrescens* complex, we carried out PCA using eight cranial variables (CBL, IO, U1B, M2B, PL, TR, UTR, MTR) measured from the holotype of *C. colombiana*, 5 *C. mera*, and 22 *C. nigrescens* from the vicinity of San Félix and Cerro Bollo in the easternmost part of that species' known range. Factor axis 1 from the PCA estimated overall size, and factor 2 represented a contrast between a heavily weighted MTR and negatively weighted U1B (table 8). In a plot of factor scores on factor axis 1 vs. factor axis 2 (fig. 19), *C. colombiana* is the largest of the three species, whereas its closest geographic neighbor, *C. mera*, is the smallest. Individuals of *C. nigrescens*, which occur furthest to the northwest geographically, overlap both of the other two species, but in general *C. nigrescens* is intermediate in size. Along the shape axis (factor 2), the three species overlap completely, reinforcing an impression of conservation of form within the *C. nigrescens* complex.

No reproductive data are available for *C. colombiana*.

Other species of mammals collected by Hershkovitz along an elevational transect from 1500 to 2100 m at the type locality of *C. colombiana* include *Dasyprocta punctata*, *Akodon* sp., *Neacomys*

TABLE 8. Factor loadings from PCA of cranial variables of *C. colombiana*, *C. mera*, and *C. nigrescens*.

Variable	Factor 1	Factor 2
UTR	0.948	-0.012
TR	0.918	0.257
PL	0.895	0.070
CBL	0.866	0.177
M2B	0.765	-0.265
IO	0.708	-0.360
U1B	0.695	-0.528
MTR	0.509	0.754

*tenuipes*, *Oryzomys albicularis*, *O. alfaroi*, *Reithrodontomys mexicanus*, *Rhipidomys latimanus*, *Thomasomys laniger*, and *Sciurus pucheranii*.

ETYMOLOGY—The specific epithet *colombiana* is derived from Colombia, the country of origin of the holotype and the only region in which this shrew is known to occur.

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## Specimens Examined

Specimens in the following list marked with an asterisk (\*) are cranial remains recovered from owl pellets. Those marked with double asterisks (\*\*) are from archeological or paleontological sites.

*Cryptotis colombiana* (1).—COLOMBIA: ANTIOQUIA: Sonsón, 15 km E of Río Negrito, 1750 m (1 FMNH—holotype).

*Cryptotis hondurensis* (3).—HONDURAS: FRANCISCO MORAZAN: 12 km WNW El Zamorano, Cerro Uyuca, 1680 m (1 KU—holotype); near San Juancito mines, 1700 m (1 FMNH); La Rosario, San Juancito, La Tigra National Park (1 UNAH).

*Cryptotis magna* (49).—MEXICO: OAXACA: La Esperanza, 1430 m (1 UAMI); Santiago Comaltepec, 1 km N La Esperanza, 1525 m (1 IBUNAM); Santiago Comaltepec, 11 km SW La Esperanza, 2000 m (25 IBUNAM); Vista Hermosa, 1600 m (2 KU); 3.5 km N Vista Hermosa, 1360 m (1 KU); 2.3 km S Vista Hermosa, 1560 m (1 KU); 12 km S Vista Hermosa, 1920 m (4 KU); 21 km S Vista Hermosa, 2080 m (1 KU); 28.6 km S Vista Hermosa, 2350 m (1 KU); 31.6 km S Vista Hermosa, Cerro Pelón, 2650 m (1 KU); 3.4 mi SSW Vista Hermosa, 6200 ft (1 KU); 6.5 mi SSW Vista Hermosa, 7100 ft (3 KU); 12 mi SSW Vista Hermosa, 9300 ft (1 KU); Llano de las Flores, 2800–2900 m (4 KU); Atepec, 13 km W Atepec, 2820 m (1 IBUNAM); Mt. Zempoaltepec (1 USNM).

*Cryptotis mayensis* (122).—BELIZE: CAYO DISTRICT: Baking Pot (1 ROM); MEXICO:

CAMPECHE: 60 km SE of Dzibalchén (19°10'N, 89°20'W) (1 ROM, 1 ASNHC); 7.5 km W of Escárcega (1 ASNHC); La Tuxpana Champotón [La Tuxpeña] (1 USNM); QUINTANA ROO: 2 km SE of Lago Chichencanab [spelled variously "Laguna Chickankanaab" (Alvarez and Martinez, 1967:205); "Laguna Chichancanab" (Choate, 1970:277; U.S. Board on Geographic Names, 1956)] (1 ENCB); 6 km S, 1.5 km W of Tres Garantías (1 ASNHC); YUCATAN: Actún Chacaljas (1 cranium\*\* AMNH); Actún Coyok, 5–90 cm (2 crania, 8 right mandibles\*\* AMNH); Actún Has, 0–85 cm (7 crania\*\* AMNH); Actún Lara, 0–130 cm (5 crania\*\* AMNH); Actún Oxkintok, 30–75 cm (3 left mandibles AMNH); Actún Spukil, owl perch (63 crania\* AMNH); Actún Spukil, excavations (3 crania, 9 right mandibles\*\* AMNH); Chichén Itzá (1 FMNH, 1 USNM—holotype); Chichén Itzá ["along the rim of the Xtolók cenote" (Hatt, 1938:334)] (1 AMNH); SW of Dzilam de Bravo (6\* IBUNAM); 2.5 km NW Dzityá (1 sui); Loltun (2\* ASNHC); Lolton [Loltun], surface of cavern floor (3 crania, 4 left mandibles\* AMNH); 6 km S Mérida (1 KU); 13 km W Peto (1 KU\*); Xbac (1 USNM).

ADDITIONAL RECORDS—GUATEMALA: PETEN: Uaxactún (Choate, 1970:277); MEXICO: YUCATAN: Buctzotz, Calotmul, Izamal, Nabalalam, Senotillo, Temax, Tzalam, Valladolid, Xbac (Gaumer, 1917); Uxmal, Mayan ruins (Alvarez and Martinez, 1967:205; Choate, 1970:277).

*Cryptotis cf. mayensis* (39).—MEXICO: GUERRERO: Zumpango del Río District, Cañon del Zopilote, 11.5 km S of the Río Mescala bridge near Mescala; Cueva de Macuiltzingo (39\* IBUNAM).

*Cryptotis mera* (7).—PANAMA: DARIEN: Cerro Tacarcuna, 4800 ft (3 USNM); Cerro Malí, 4700 ft (1 USNM); Mount Pirri [Cerro Pirre], E slope near head of Río Limón, 4500–5000 ft (3 USNM—including holotype).

*Cryptotis merriami* (29).—COSTA RICA: GUANACASTE: 4.5 km NE of Tilarán (1 KU). EL SALVADOR: MORAZAN: Mt. Cacaguatique, north slope, 3800–4000 ft (3 MVZ); SAN MIGUEL: Mt. Cacaguatique, 3500–4000 ft (8 MVZ, 2 UMMZ). GUATEMALA: ALTA VERAPAZ: La Primavera (1 AMNH); Tucurú, Hacienda Concepción, 1100 m (1 UMMZ); San Pedro Carchá (1 ENCB); HUEHUETENANGO: Barillas, Hacienda Santa Gregoria (1 UMMZ); Jacaltenango, 5400 ft (4 USNM—including holotype). HONDURAS: EL PARAI-SO: Yuscaran, Monserrat [Cerro de Moncerrato]

Cloud Forest (1 MCZ); FRANCISCO MORAZAN: La Tigre National Park, San Juancito, La Rosario (1 UNAH); LEMPIRA: Las Flores Gracias (1 AMNH); SANTA BARBARA: San José (1 AMNH). MEXICO: CHIAPAS: Volcán Kagchiná, 3.5 km N Las Margaritas, 1500 m (2 MHP\*). NICARAGUA: MATAGALPA: 9 mi N of Matagalpa, Santa María de Ostuma, 1400 m (1 UMMZ).

ADDITIONAL RECORDS—EL SALVADOR: AHUACHAPAN: 2 mi NW Apaneca (Burt and Stirton, 1961). GUATEMALA: ALTA VERA-PAZ: La Primavera, 3200 ft (Choate, 1970:279). MEXICO: CHIAPAS: Cueva Los Llanos, 9 km S Las Margaritas, 1500 m (Choate, 1970:279).

*Cryptotis nigrescens* (119).—COSTA RICA: ALAJUELA: Cinchona, 1600 m (1 KU); Monteverde Cloud Forest Reserve, 1580–1600 m (3 KU); Monteverde Cloud Forest Reserve, Peñas Blancas Valley, 870 m (2 KU); ALAJUELA/GUANACASTE border: Monteverde Cloud Forest Reserve, 1580 m (1 KU); CARTAGO: [Volcán] Irazú, 8000–9400 ft (1 AMNH); GUANACASTE/PUNTARENAS border: near Monteverde, Cerro Amigos, 1750–1790 m (3 KU); PUNTARENAS: Coto Brus [Canton], Sabalito District, Las Tablas, Río Cotón, 1700 m (1 MNCR); Monteverde, 1345–1600 m (3 FMNH, 1 INBIO, 24 KU, 3 LACM, 1 MMNH, 7

UMMZ); Monteverde Cloud Forest Reserve, 1530–1660 m (5 KU); San Luis, 1200 m [ca. 2.5 km S Monteverde] (1 KU); 1 mi SW of Finca Las Cruces, San Vito, 4000 ft (3 LACM); SAN JOSE: San Isidro (1 AMNH—holotype); 9 mi N of San Isidro del General (Pan American Highway), 4800 ft (1 UMMZ). PANAMA: BOCAS DEL TORO: Fish Camp, 4900 ft (8°58'N, 82°40'W) (2 USNM); El Volcán [Hato del Volcán] (4 USNM); 19 km NNW of El Volcán, E of Cerro Pando, 8°56'30"N, 82°42'15"W, 6400 ft (1 USNM); Volcán de Chiriquí, Río Candela, 6000 ft (2 AMNH); 25 km NNE of San Félix, 1425–1500 m (5 USNM); BOCAS DEL TORO/CHIRQUI border: Cerro Bollo, 3.5 km E Escopeta, which latter is at ca. 23 km NNE San Félix, 1800–1856 m (14 USNM); CHIRQUI: Cerro Punta (1 USNM); Cerro Punta, 6500 ft (1 USNM—holotype of *C. zeteki*); Cerro Punta, 2700 ft (2 USNM); Cerro Punta, Boquete Trail, 6800 ft (1 USNM); 24 km NNE of San Félix, 1275–1350 m (6 USNM); 24.5 km NNE of San Félix, 1325–1350 m (2 USNM); 14.5 km NW of El Volcán, Finca Santa Clara, 8°51'30"N, 82°44'45"W, 1200–2150 m (12 USNM); Santa Clara, Volcán de Chiriquí, 1700 m (3 USNM); Santa Clara, on the Pan American road 15 mi from Costa Rica, 4200 ft (1 AMNH—holotype of *C. tersus*).



















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